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NATURAL SELECTION AND FAMILY SIZE IN THE STARLING

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INTRODUCTION

It is extremely difficult to measure natural selection in the field because, when one variant is at a marked disadvantage compared with another, it is usually too rare to provide adequate data, while when both variants are common, their selective value is closely similar (except where a heterozygote is at an advantage compared with either homozygote). It might seem especially rash to attempt to study such a problem in the case of clutch-size in birds, when the genetic factors controlling it are unknown. However, clutch-size possesses one characteristic which facilitates such an investigation, due to the fact that it directly affects the number of offspring. The point in question can be made clear by a hypothetical (and over-simplified) example. Suppose that a species consists of two hereditary types, one laying 5 and the other 6 eggs in a clutch. If both types are common, both presumably have an almost equal selective value, and each gives rise to about the same eventual number of descendants, which means that their offspring should survive in the ratio of 6:5, a difference which might be large enough to demonstrate in the field.

A preliminary review of the clutch-size problem has been published elsewhere (Lack, 1946, 1947–8). It was there pointed out that the limitation of clutch-size to a comparatively small number of eggs cannot be adequately explained on purely physiological grounds. The view that it is adjusted to the mortality of the species is also untenable. The alternative hypothesis was put forward that it is ultimately selected by the number of young which the parents can raise, the latter being determined by the available food supply. This view, so acceptable *a priori* to the population-geneticist and so difficult, apparently, for the traditional ecologist, was supported by much circumstantial evidence, chiefly relating to seasonal and regional trends of variation in clutch-size.

In the present paper, an attempt is made to provide direct evidence, to test whether, in fact, the young from broods of large size are at a disadvantage compared with those from broods of small size. It might be expected that, for broods above the average size, proportionate mortality among the young would rise as brood-size increased. When this is so, a point is quickly reached where an increase in the number of eggs is offset by the increased mortality, so that there is no increase in the number of young raised. One might reasonably hope to

find evidence for this turning point in nature. However, one could not expect to go beyond it, to the point when productivity actually declines with increasing clutch-size, as deleterious mutants tend to be eliminated, hence individuals with disadvantageously large clutches would tend to be very rare. It should be added that even the turning point might be obscured if there were extensive non-genetic modifications in clutch-size, as shown in the parallel case of litter-size in mammals (Lack, in press).

The Raw Data

The European Starling (*Sturnus vulgaris*) was selected for study, as the data were more extensive and less complex than for other species, which will be treated in later papers. The data used here come from: (i) Institute for Plantenziektenkundigen Dienst, Wageningen, Holland, for clutch-size and nesting success; (ii) Vogelwarte Sempach, Switzerland, for brood-size and post-fledging survival; (iii) Edward Grey Institute, Oxford, for clutch-size, in MSS by R. Carrick, A. Whitaker, late F. C. R. Jourdain, and the British Trust for Ornithology Hatching and Fledgling Enquiry; (iv) *British Birds* and British Trust for Ornithology Marking Scheme, for brood-size and post-fledging survival. The writer is particularly indebted to Dr. Kluijver in Holland and Dr. Schifferli in Switzerland for generously putting their extensive data at his disposal, when it was found that the British data were insufficient.

Clutch-Size

In Britain, Holland and Switzerland, the Starling lays its first clutch in April or early May. A smaller number of layings occur in late May and in June, these being due partly to one-year-old birds breeding for the first time, partly to older birds whose first layings were destroyed, and partly to older birds which have already raised one brood in the season. In this paper, all clutches laid in April, and all broods with young old enough to band in May, have been classified as "early" broods, and they have been separated from later layings, which are on the average somewhat smaller in size. The latter point is shown for clutch-size in Holland in table 1, and for brood-size in all three regions in table 2. The differences are statistically significant. In general, 5 is the commonest size of an early laying, and 4 of a late clutch.

Table 1. *Clutch-size*

Clutch-size	Number of clutches in		
	N. England	Holland	
	April	April	June
1		1	2
2	1	10	5
3	7	41	28
4	29	273	80
5	47	669	64
6	12	447	10
7	6	131	4
8	3	17	
9		1	
10		2	
Total	105	1592	193
Average	4.9	5.2	4.3

Note. Average clutch-size for May layings in Holland was 4.9.

The Starling also shows a regional variation in clutch-size. As in many other passerine species, average clutch-size is somewhat smaller in England than in central Europe at the same latitude (Lack, 1947–8). This is shown for clutch-size in England compared with Holland in table 1, and for brood-size in England compared with Holland and Switzerland in table 2. The average differences are rather smaller than those associated with the season of the year, but are statistically significant.

Parental Feeding Rate

The hypothesis of this paper rests on the assumption that the parent Starlings bring less food to each nestling in a large than a small brood. This was found by

TABLE 2. *Brood-size*

Brood-size	Number of early broods in			Number of late broods in		
	N. W. England	Holland	Switzerland	N. W. England	Holland	Switzerland
1	?	30	65	?	34	44
2	66	98	164	31	77	96
3	166	189	426	66	145	254
4	311	395	989	57	194	391
5	295	425	1235	25	124	285
6	69	196	526	4	29	73
7	6	41	93		14	7
8		3	15			
9			2			
10			1			
Total	913	1377	3516	183	617	1150
Average	4.1	4.4	4.5	3.3	3.7	4.0

Notes. (i) The English average has been adjusted to allow for the fact that broods of 1 are not recorded, by assuming that the ratio of broods of 1 to broods of 2 is the same as in Switzerland and Holland.

(ii) The average for all 2186 English broods banded in May was 3.9 and for 538 later broods it was 3.0—these figures are rather smaller than those for N.W. England only.

(iii) The Swiss averages are: for May: 4.5, first half of June: 4.1, second half of June: 3.8 and July: 3.5, based on 3516, 439, 580 and 131 broods respectively.

TABLE 3. *Feeding frequency and brood-size (after Kluijver)*

(i) 1930

Days after hatching	Number of feeding visits per day for brood of 4	brood of 6
3	208	227
4	247	235
5	251	306
6	303	306
7	345	476
8	300	525
9	388	430
10	358	448
11	240	472
12	401	483
13	395	485
14	358	440
15	366	408
16	421	366
17	378	393
Total in 15 days	4959	6000
Total per nestling per day	83	67

(ii) 1931

	brood of 2	brood of 6
Total of feeds per day	224	390
Feeds per day per young	112	65

Note. The first set of records is adapted from Kluijver (1933), table IV, p. 57, and the second set from his table III, p. 55.

Kluijver (1933) to hold in the Starling, as summarised in table 3, but further data on this point are desirable. However, a similar result was obtained for most other species in which this problem has been investigated by Moreau (1947). To summarise these data: with a brood of larger size, the parents increase the number of their feeding visits, but the increase is not sufficient to offset the larger number of young, so that each nestling is fed less often in a large than in a small brood.

MORTALITY IN THE NEST

Owing to the above fact, it was expected that the young would show, on the average, a proportionately higher mortality in large than small broods. The nesting data for the Starling in Britain did not suggest this, but were too few for analysis. Fortunately, extensive nest records are available from Holland since 1922, in the form of the number of eggs laid and the number of young alive on the observer's last visit. These are analysed in table 4, and show decisively that the above expectation is not realised.

TABLE 4. *Nesting success (egg–fledgling) in Holland*

Clutch-size	Number laid		No. fledged	Per cent fledged	
	All broods	All broods except total failures	All broods	All broods	All broods except total failures
1. April layings					
3	126	105	86	68	82
4	956	864	727	76	84
5	2975	2770	2324	78	84
6	2298	2184	1784	78	82
7	798	756	620	78	82
8	120	112	87	73	78
others	55	53	34	—	—
Total	7328	6844	5662	77	83
2. Late layings					
3	162	144	125	77	87
4	888	800	642	72	80
5	1345	1210	949	71	78
6	516	486	340	66	70
7	245	203	159	65	78
others	73	71	46	—	—
Total	3229	2914	2261	70	78

Notes. (i) "Total failure" refers to broods in which no nestling fledged. It is better to omit losses of entire broods, as these are due mainly to predation and are erratic.

(ii) Number "fledged" means number of young alive in nest on observer's last visit; each nest was visited at least weekly.

As interest is in mortality due to malnutrition, losses of entire broods are better omitted from analysis, since they are due mainly to predation, including human destruction. The right-hand column of table 4 shows that, in early layings, the proportion of eggs which give rise to fledged young is approximately the same for clutches of 3, 4, 5, 6, 7 and 8 eggs. For late layings, the answer is similar; (except for an apparent lower success for clutches of 6, which is attributable merely to random sampling, as a similar drop is not found for clutches of 7). When the losses of entire broods are included in the analysis (fifth column of table 4), the results for early layings again show no variation with clutch-size, and the apparent variation in late layings is doubtless due to random sampling, the losses of entire broods being very erratic in their incidence from place to place and year to year. Nestling mortality was found to be independent of brood-size in the four other small passerine species in which this point has been studied (Lack, 1946, and unpublished).

NESTLING WEIGHT

The fact that nestling mortality is similar for broods of different sizes was first discovered for the Robin (*Erithacus rubecula*) (Lack, 1946). To investigate the problem further, nestling Robins were weighed daily from hatching to flying. This unexpectedly revealed that there were extremely marked individual variations in the weight of the nestlings (Lack and Silva, in press; Lees, in press). Lees (in litt.) has found similar large variations in the other small passerine species which he has weighed. In such species, the nestling can remain alive, and develop its feathers normally, although badly under weight, and the chief effect of undernourishment on a nestling is not death in the nest, but a reduced weight when it leaves the nest. The only comparative data so far available on the weights of nestling Starlings in broods of different sizes were obtained in 1947 by R. Carrick

TABLE 5. *Nestling weights of Starling*
Obtained in England in May 1947, by R. Carrick

Age in days	Average weight per nestling in grams in		
	Brood of 2	Brood of 5	Brood of 7
4	28.8	—	21.4
6	48.3	45.1	38.2
15	88.0	77.6	71.4

Note. The limits of weight on day 15 were for brood of 2: 87.5–88.5; for brood of 5: 72.5–83.0; and for brood of 7: 66.0–77.0.

for three broods of different sizes, all raised by fully adult parents, all in the same locality, and all starting incubation on the same date. The results, set out in table 5, fit the view that the average nestling weight decreases as brood-size increases, but many more data are needed before this point can be considered established.

Post-Fledging Survival in Switzerland

Those young which are below normal weight on leaving the nest might well have a reduced chance of subsequent survival. Moreover, any differences in their fledging weight associated with size of brood would tend to be intensified in the period immediately after leaving the nest, when the young are still dependent on their parents for a time; hence the greater the number of young, the less often each will tend to be fed. This means that the possible adverse effects of a large brood-size on survival can be revealed only if the data are extended to cover the period after leaving the nest.

Soon after leaving the nest, young Starlings join with their parents to form large flocks, and it would seem impossible to study the further fate of individual broods in the wild. However, the essential data can be obtained indirectly from bird-banding, which was originally started to study migration, but has since thrown light on many other points of biological interest. For the Starling, the Swiss data are particularly extensive, and most observers recorded the number of young separately for each brood banded.

Should there be, in the period shortly after leaving the nest, a heavier mortality among the young from large than from small broods, then proportionately more individuals from small than large broods should survive to maturity. The proportion of young Starlings from each brood-size alive at the time of leaving the nest is easily (if laboriously) obtained by adding up the numbers of all banded young, separately for each brood-size. The proportion of successful survivors from each brood-size is revealed by adding up the number of individuals from each brood-size recovered after they have attained a certain age. The minimum age for such 'successful survival' was provisionally fixed at three months after leaving the nest, and the results indicate that, in fact, the main mortality due to any undernourishment in the nest has occurred before this age is reached. N. B. It does not matter whether the birds recovered after reaching this age were found dead or alive since the point of interest is whether they successfully attained this age. In fact, most of the Swiss birds were recovered dead, the Dutch alive, while the British sample included many of both types.

The brood-size of a recovered Starling is, of course, found by turning up the band-number concerned in the original banding data. Only about 2% of the banded nestling Starlings are later recovered. The rest die undetected. The assumption is made here that those recovered more than three months after they leave the nest are a random sample of the population remaining alive. (The individuals recovered within the first three months come in a different category, and will be discussed later.)

The results set out in table 6 are highly suggestive. In early broods, 5 is the commonest size of family. The recovery-rate for birds more than three months out of the nest is about the same for those coming from broods of 3, 4 or 5 young, in each case being around 2%. On the other hand, as soon as the brood-size exceeds 5, the recovery-rate falls. For individuals from broods of 6 it is only 1.7%, and for those from broods of 7–8 it is only 1.4%. If, now, the proportion of individuals recovered is multiplied by the original number of young in the brood (as in the right-hand column of table 6), it is seen that, on the average, a brood of 5, 6 or 7 young gives rise to the same number of recoveries, about 0.1 per brood. If these recoveries are representative of the population,

TABLE 6. *Post-fledging survival in relation to brood-size. For Swiss Starlings banded as young*

Brood-size	No. of broods banded	No. of young banded	Young recovered more than 3 months after fledging		Relative productivity (previous column • × brood-size)
			Number	Percentage	
1. Early broods (banded in May)					
1	65	65	0	—	—
2	164	328	6	1.8	3.7
3	426	1278	26	2.0	6.1
4	989	3956	82	2.1	8.3
5	1235	6175	128	2.1	10.4
6	526	3156	53	1.7	10.1
7	93	651	10	1.5	10.2
8	15	120	1	0.8	
9	2	18	0	—	—
10	1	10	0	—	—
Total	3516	15757	306	1.94	
2. Late broods (June, July)					
1	44	44	1		
2	96	192	8	2.3	5.8
3	254	762	14		
4	391	1564	35	2.2	8.9
5	285	1425	25	1.8	8.8
6	73	438	6	1.4	8.2
7	7	49	—	—	—
Total	1150	4474	89	1.99	

this must mean that an increase in brood-size between 5 and 7 young is approximately counterbalanced by an increase in proportionate mortality among the young, taking place in the period shortly after they leave the nest. (Broods of 9 or 10 young are too scarce for a reliable estimate of their mortality. This scarcity suggests that they are at a selective disadvantage, with productivity below that of broods of smaller size, but this view could be tested only by the experimental addition of young to nests, so as to make up a large series of broods of 9 and 10 young artificially.)

The above data fit the hypothesis advanced earlier, viz. that when brood-size rises above the average, mortality also rises, so that productivity is not increased. Unfortunately, the proportion of birds recovered is so small that, despite the large numbers banded, the totals recovered are too small for the apparent differences in recovery-rate to be statistically significant. One could not expect bigger differences in the recovery-rates than those actually obtained, since, according to theory, the productivity per brood should be about equal for a brood of 5, 6 or 7 young, as in fact it is. (Had the young from broods of 6 or 7 survived less well, broods of 6 and 7 would have been less productive than broods of 5, and so would presumably have been extremely scarce.) Hence the lack of a significant result is due to the small number of recoveries, and not to the size of the difference found. For a significant result, about twice the

present number of recoveries is needed, on the assumption that they are recovered in the same proportions as in table 6. The Swiss are now resuming the intensive banding of Starlings, which was stopped in 1937, but it may be another decade before sufficient further data have been obtained.

Turning to the second half of table 6, in late broods 4 is the commonest size of family, and the recovery-rate falls from 2.2% in broods of 4, to 1.8% in broods of 5, and to about 1.4% in broods of 6. Once again, if the proportion of individuals recovered is multiplied by the number of young in the brood, it is seen that broods of 4, 5 and 6 young are about equally productive. Hence the results from late broods corroborate those from early broods. Unfortunately, the data are again too few for the result to be statistically significant.

In both early and late broods, the decline in survival-rate appears to commence as soon as brood-size rises above the commonest size found in nature (as theory requires), and it is interesting that this brood-size is one smaller in late than in early broods. Table 6 shows that the young from late broods have a similar *total* recovery-rate to those from early broods, i.e., 1.99% cf. 1.94%, but this equality is achieved only because the average size of late broods is smaller by one. For broods of 5 young or more, the survival-rate is lower in late than early broods. This strongly suggests that the reduction in average clutch-size in late as compared with early layings is an advantageous adaptation, and it may be suggested that the food supply available for nestling Starlings is smaller late than early in the season. Kluijver (1933) showed that, though the food is highly variable, the young of early broods are fed mainly on dipterous larvae, those of late broods mainly on Orthoptera. The latter possibly provide a less available or less nutritious diet than the former, but this point requires investigation, as does the regularity of the above difference in diet.

An independent check on the results in table 6 is provided by those banded Starlings found dead within three months of leaving the nest. As those in their third month might already have survived the period in which death occurs through previous undernourishment as a nestling, it is better to restrict analysis to the first two months after leaving the nest. As before, only a small proportion of the banded young which die in this period are later found and reported. These dead birds might be a random sample of the population alive at the time, in which case one would expect the recoveries to be in roughly the same proportions as the birds originally banded. Alternatively, the sample might include some of those juveniles dying as a result of undernourishment, in which case one would ex-

TABLE 7. *Recoveries of birds dead within 2 months of leaving nest*

Brood-size	For Swiss Starlings banded in May			
	No. banded	No. found dead in		Per cent found dead less than 2 months old
		1st month	2nd month	
1	65	—	—	0.21
2	328	—	—	
3	1278	—	2	
4	3956	2	8	
5	6175	14	8	0.35
6	3156	9	5	0.43
7	651	1	2	
8–10	148	—	—	
Total	15757	26	25	0.32

Notes.
(i) The differences in recovery-rate are not significant.
(ii) Recovered in 3rd month: 2 from broods of 4, 6 from broods of 5, 1 from broods of 7.
(iii) Recoveries from late broods: in first two months, 3 from broods of 2, 5 from broods of 3, 4 from broods of 4 and 4 from broods of 5: in third month, 1 from brood of 3, 1 from brood of 4, 2 from broods of 5, and 1 from brood of 6.

pect to find a relatively high proportion of individuals from broods of sizes above the average. On neither view, however, would one expect to find a relatively high proportion of dead individuals from broods of small size, such as occurred in table 6.

The data for early broods in table 7 indicate that, during the first two months after leaving the nest, there is a higher recovery-rate of dead young from broods of large than small size, i.e., the reverse of table 6. This therefore supports the view that the young from broods of larger size are at a comparative disadvantage in the period soon after leaving the nest. Unfortunately, the recoveries are again too few to give a result which is statistically significant. (The data for late broods are too few to be worth analysing, but are added as a footnote to table 7.)

British and Dutch Data

Many fewer Starlings have been banded, and a smaller proportion recovered, in Britain than in Switzerland. The results for those recovered after they are three months old are set out in table 8, and, in general, support those from Switzerland in table 6, though once again they are too few to show whether the apparent differences in recovery-rate are statistically significant. For early broods in Britain, 4 is the commonest size of family, and the recovery-rate for individuals from broods of 4 is 1.9%, whereas for individuals from broods of 5–7 it falls to only 1.6%.* In late broods, the commonest size of family is 3, and the recovery-rate is smaller from broods of 4 and 5 young than from broods of 3.

Table 8. *Recoveries of British banded Starlings*

Brood-size	No. of broods banded	No. of young banded	Young recovered more than 3 months old		
			Number	Percentage	
1. Early broods (May)					
2	255	510	7	1.5	
3	455	1365	22		
4	734	2936	55	1.9	
5	596	2980	44	1.5	
6	133	798	17	2.1	1.6
7	13	91	2		
Total	2186	8680	147	1.7	
2. Late broods (June, July)					
2	120	240	3	c.1.3	
3	191	573	19	3.3	
4	165	660	14	2.1	
5	54	270	1	c.0.3	
6	7	42	—	—	
7	1	7	—	—	
Total	538	1792	37	2.1	

Note. The apparent higher recovery rate from late than early broods is probably due to chance, as it mainly results from one worker's trapped recoveries. When his recoveries are omitted, the proportions recovered are 1.3% for May and 1.5% for late broods.

The recovery-rate for Starlings in their first two months after leaving the nest is much higher in Britain than in Switzerland; hence despite the smaller totals banded, there are enough British recoveries from early broods for a significant result. The data in table 9 show that, in the first two months after leaving the nest, the recovery-rate is significantly higher for dead young from broods above the average in size than for dead young from broods of smaller size. This confirms the results in table 7, and supports the view that the young from broods of above average size experience a heavier mortality than those from broods of smaller size,

* The apparent higher survival rate for British Starlings from broods of 6–7 than from broods of 5 is presumably due to random variation in a small sample. It might be added that in 1933 one man, H. J. Moon, banded 11 broods of 6 young each, from which 5 individuals were later recovered, a very high proportion. For all other years and all other brood-sizes, Moon's recovery-rates were normal. Omitting his 1933 data, the proportion recovered from British broods of 6 is only 1.6%, a much more reasonable figure.

TABLE 9. *Recoveries of birds dead within 2 months of leaving nest. For British Starlings banded in May*

Brood-size	No. banded	No. found dead in		Per cent found dead less than 2 months old
		1st month	2nd month	
2	510	3	1	0.42
3	1365	3	2	
4	2936	9	2	
5	2980	18	6	0.78
6	798	3	2	
7	91	1	—	
Total	8680	37	13	0.58

Notes. (i) The difference in recovery-rate for smaller compared with larger broods is significant, $\chi^2 = 4.8$.
(ii) Recoveries in 3rd month: 1 from brood of 2, 1 from brood of 3, 4 from broods of 4, and 2 from broods of 5.
(iii) Recoveries from late broods: in first 2 months, 4 from broods of 2, 6 from broods of 3, 6 from broods of 4, and 5 from broods of 5: in third month, none.

during the first two months after they leave the nest.

A few data are also available from Holland, all obtained from broods banded in the last week of May, 1932 and 1933, by H. N. Kluijver. The high rate of recovery is due to the fact that most recoveries were of individuals trapped alive at nest-sites in a later year. In Holland, as in Switzerland, 5 is the commonest brood-size, and the data in Table 10 show that successful survival to an age of at least 3 months is proportionately much higher for young from broods of 5 or less, than it is for young from broods of more than 5 young. The difference is statistically significant.

To sum up the results in tables 6–10, in Switzerland, Britain and Holland, the differences in survival-rate among the young from broods of different sizes support the hypothesis advanced *a priori*, although in only two cases (tables 9, 10) are the differences statistically significant. However, there are altogether seven independent analyses, five for young attaining an age of at least three months (viz. Swiss early and Swiss late broods, British early and British late broods, Dutch early broods), and two others for young dying in the first two months (viz. Swiss early and British early broods). All seven analyses give an answer in accordance with the view that, for broods above the average in size, juvenile mortality is higher; hence, taken together, they strongly suggest that this view is correct.

TABLE 10. *Recoveries of Dutch Starlings banded in May*

Brood-size	No. of broods banded	No. of young banded	Young recovered more than 3 months old	
			Number	Percentage
2	3	6	—	10
3	5	15	2	
4	16	64	6	
5	45	225	24	
6	25	150	5	3
7	3	21	1	
8	1	8	—	

Note. The difference in recovery-rate for smaller as compared with larger broods is significant, $\chi^2 = 6.7$.

THE REGIONAL DIFFERENCE

It will be noted that in early broods the commonest number of young is 5 in Switzerland but only 4 in Britain, while in late broods it is 4 in Switzerland but only 3 in Britain. Lack (1947) showed that there was a widespread tendency for the average clutch-size of passerine birds to be larger in Central Europe than in Britain at the same latitude, and argued that a general trend suggests an adaptation. The data in tables 6 and 8 fit in with this suggestion, since, in early broods, the survival-rate begins to decrease with a brood of more than 5 young in Switzerland, but with a brood of more than 4 young in Britain, while in late broods the decrease commences with a brood of more than 4 young in Switzerland but with a brood of more than 3 young in Britain.

This presumably means that more food is available for young Starlings in Switzerland than in Britain, but there are as yet no data on this point. In the parallel case of the Swift (*Apus apus*) in the two regions, there is suggestive evidence that not only average clutch-size but also food supply is greater in Switzerland than in Britain (Lack and Arn, 1947).

Lack (1947) also showed a general tendency in passerine birds for average clutch-size to be higher in the north than the south of the European range. There are not yet sufficient data on this point for the Starling (but see note to table 2).

Adaptive Modifications

Although clutch-size might be regarded as a form of polymorphism, the discontinuities are due to the impossibility of laying fractions of an egg, and the hereditary control is probably influenced by a number of genes, as in the case of other quantitative characters, such as body-size. The frequency distribution of clutch-sizes suggests a roughly normal curve.

A further complication is the existence of non-genetic, adaptive modifications. In birds, three important advantageous modifications in clutch-size have been demonstrated, connected with (i) season of year, (ii) age of bird and (iii) differences in feeding conditions from one year to another (Lack, 1947).

(i) In the Starling, the seasonal variation has already been discussed, and there is suggestive evidence that the smaller size of late broods is adaptive. Similarly in the Alpine Swift (*Apus melba*), late clutches are smaller than early clutches, and it has been shown that the survival-rate from broods of large size is smaller in late than it is in early broods (Lack and Arn, 1947).

(ii) Kluijver (1933, 1935) has shown that Starlings breeding for the first time, when about a year old, tend to lay clutches of smaller average size than do older parents. A similar tendency is found in other passerine and near-passerine species (Lack, 1947; Lack and Arn, 1947), and it is probably general. It seems reasonable to consider this as another advantageous modification, which has become part of the hereditary constitution of the species through natural selection, due to the fact that parents breeding for the first time are less efficient at collecting food for nestlings than are experienced parents, so that the optimum brood-size is somewhat smaller for young than for experienced parents. This supposition has not as yet been tested for any species, and should be investigated.

This second modification means that, unless first-year parents can be separated from the rest, the results of an analysis such as that in table 6 will be somewhat obscured. For some of the broods of small size will be those raised by first-year and inexperienced parents, and their young may have a smaller chance of subsequent survival than have the young from broods of rather larger size raised by experienced parents. In the Starling, however, unlike some other species, Kluijver (loc. cit.) has shown that many of the first-year birds breed later in the season than the older birds, so that the first broods of the latter are usually separated from the former by date alone. Probably most of the early (i.e., May) broods whose survival was analysed in tables 6 and 8 were raised by experienced parents.

(iii) A few passerine species show marked, and others small, differences in average clutch-size from one year to another. A variation of this nature has presumably become a characteristic of the species only when, on balance, it is advantageous. The advantage is obvious in the case of African passerine species which have larger clutches when the rains are heavy (Moreau, 1944), and in the case of rodent predators which have larger clutches when there is a vole or lemming plague (Lack, 1947). There is also suggestive evidence that, in the Alpine Swift, the years of larger average clutch-size are also the years with high nesting success

among broods of large size (Lack and Arn, 1947).

Kluijver's data for the April layings of the Starling in Holland are analysed in table 11 for each year separately. The low averages for 1922 and 1925 are possibly doubtful, as in a co-operative study the accuracy of the observers tends to increase with time. However, even omitting the early years, average clutch-size varies between 5.06 in 1931 and 5.55 in 1930, and an analysis of variance shows that the differences in mean are greater than can be attributed to chance alone. There therefore seems to be some annual variation in the size of the first layings of the Starling. The laying time varies from one year to another, associated with the general earliness or lateness of the spring, but the data in table 11 show that this is not the major cause of the clutch-size variation. For the present, the latter cannot be explained, nor is it known whether it is an advantageous modification. It should be added that it is much smaller in extent than in some other species. Extensive adaptive modification have a highly obscuring effect on the type of analysis undertaken in table 6, since small clutches tend to be laid when conditions are unfavourable for the survival of the young, and large clutches when they are favourable. In an extreme case, with much phenotypic and no hereditary variation in clutch-size, one would expect proportionate survival to be very similar from clutches of all sizes. This point has been discussed in mammals (Lack, in press) and will be discussed later for other species.

TABLE 11. *Annual differences in average clutch-size*

In Holland

Year	No. of nests	Mean clutch-size	S.E.	Mean date of laying of first broods
1922	29	4.79	0.19	—
1923	51	5.29	0.14	22.IV
1924	52	5.37	0.14	28.IV
1925	82	4.76	0.11	20.IV
1928	85	5.28	0.11	30.IV
1929	12	5.42	0.29	4.V
1930	106	5.55	0.09	22.IV
1931	196	5.06	0.07	26.IV
1932	116	5.41	0.09	29.IV
1933	245	5.09	0.06	25.IV
1934	228	5.27	0.07	23.IV
1935	138	5.39	0.09	24.IV
1936	239	5.39	0.06	25.IV
1937 & 42	13	5.00	0.28	—
All years	1592	5.24		

Notes. (i) Variance ratio = 4.69/1.00 at 13/1578 degrees of freedom, which is significant. The result is still significant if the first four years are omitted from consideration.

(ii) The mean date of laying was calculated for that of all clutches laid before May 10th each year.

Table 11 shows that each individual Starling does not necessarily lay a clutch of the same size in each year, and this is confirmed by data from H. N. Kluijver on the layings of marked individuals in successive years, set out in Appendix I. The data are restricted to first broods, late broods being omitted. Layings of individuals known to be only one year old are also omitted, though some may have been included inadvertently, as most of the birds were of unknown age when banded. Analysis shows that the variance between clutches of the same individual is smaller than the variance between clutches of all individuals, the difference being statistically significant at a probability of .01. Hence, despite some annual variation, each individual has a tendency to lay a clutch of similar size each year (after the first). This accords with the view that clutch-size has a hereditary basis. Data given by Nice (1937) for the Song Sparrow (*Melospiza melodia*), and by Weitnauer (1947) and Lack and Arn (1947) for Swifts (*Apus* spp.), suggest a similar conclusion for these species, but more detailed observations are needed.

Recoveries from the Same Brood

Table 12 shows the number of cases in which two members of the same brood were later recovered, this being confined to cases in which both individuals attained

TABLE 12. *Recoveries from same brood*

Brood-size	No. of broods banded	No. of recoveries over 3 months old	No. of cases of 2 in same brood
Switzerland			
2	260	14	1
3	680	40	—
4	1380	117	7
5	1520	153	10
6	599	59	3
7	100	10	—
8–10	18	1	—
Britain			
2	375	7	—
3	646	28	1
4	899	39	2
5	650	29	2
6	140	12	—
7	14	1	—
Holland			
2–3	8	2	1
4	16	6	—
5	45	24	4
6	25	5	1
7–8	4	1	—

Notes. (i) For Britain, recoveries of birds trapped are omitted.
(ii) In Switzerland, one pair was due to trapping in the same place.
(iii) In Switzerland, there were 6 further cases (omitted in table 12) in which one of the pair was recovered in its 2nd month of life.

an age of at least three months. The number of such pairs recovered is higher than would be expected by chance, and the departure from random is significant. This result is not attributable merely to a tendency for birds in the same brood to stay in the same flock, as the two recoveries were usually from widely separated localities, for instance one from Algeria in winter and the other from Switzerland in summer. A similar tendency is also apparent among British Starlings. To test the latter, all trapped recoveries were omitted, as these come from a few restricted localities, which increases the chance of finding two in the same brood.

The above result could be explained through a tendency for either all or none of the members of each brood to survive the dangerous first three months of life. Such a tendency might occur if the parents fed each nestling in the brood about equally, so that either all or none of them tended to be undernourished at the time of leaving the nest. This point could be studied further by a detailed analysis of nestling weight in the Starling. It will be shown later that, in Song Thrush (*Turdus ericetorum*) and Blackbird (*T. merula*), the frequency with which two individuals from the same brood are recovered is about what would be expected by chance, and there is no tendency of the type shown in table 12. In the Great Tit the same tendency is found as in the Starling, but in this species nearly all the recoveries are due to trapping in restricted localities, so that this result might merely reflect the tendency for individuals from the same brood to stay in the same flock.

POPULATION TURN-OVER

It is seen from table 2 that the Starling has a lower reproductive rate in Britain than in Switzerland. While in both countries the Starling has been increasing in numbers in the last fifty years, the increase has probably been sufficiently slow to mean that the average number of young born each year is very nearly equal to the average annual mortality. The higher reproductive rate of Swiss than of British Starlings should therefore mean that the Swiss birds have a higher annual mortality than the British. This point can be tested by analysing the age at death of each banded bird later recovered, as set out in table 13. This indicates that the mortality in the first year is 73% for Swiss but only 66% for British Starlings, while in later years it is 62% for Swiss and only 55% for British birds. These differences are statistically significant, and therefore support the above hypothesis. However,

TABLE 13. *Annual mortality of banded Starlings in Switzerland and Britain*

Year	Number found dead in Switzerland	Britain
1st	433	261
2nd	97	75
3rd	45	26
4th	8	23
5th	7	6
6th	1	3
7th	—	—
8th	—	1
12th	1	—
Total	592	395
Mortality in first year	73%	66%
Average annual mortality after first year	62%	55%

Notes. (i) For Starlings banded as young, the first year is reckoned from date of ringing to May 31st of following year, and subsequent years from June 1st–May 31st.

(ii) Average annual mortality is given by $\frac{D2 + D3 + D4 \cdots}{D2 + 2D3 + 3D4 \cdots}$ where D2, D3, D4 = no. of young found dead in 2nd, 3rd, 4th, ··· years after ringing.

(iii) The mortality data are analysed in more detail elsewhere (Lack and Schifferli, in press).

it is possible that the small percentage of recovered Starlings is slightly biassed as to age, as discussed in greater detail by Lack and Schifferli (in press). It is scarcely necessary to add that, in a balanced population, a higher mortality-rate is an inevitable result of a higher reproductive rate. The types of danger to which Swiss and British Starlings are respectively subjected are a purely secondary consideration.

CONCLUSION

The data in this paper suggest that, as brood-size increases, the mortality among the young also increases, in such a way that the commonest brood-size found in nature is also the size with optimum productivity. This result appears to hold under the differing seasonal conditions of first and late broods, and the differing regional conditions of Switzerland, Holland and Britain. The facts therefore support the view that clutch-size is determined by natural selection acting through the survival of the young.

However, while the position may be regarded as satisfactory thus far, many difficulties remain. The most important gap in knowledge, and one that will be difficult to fill, is the way in which clutch-size is inherited. Knowledge of this is essential before a really adequate formulation can be achieved. Another difficulty in the present analysis is the persistence of many clutches of 4 in early layings of the Swiss Starling. The survival of individual young from broods of 4 appears to be no better than the survival of individual young from broods of 5; hence the productivity from broods of 4 is lower than that from broods of 5 (see table 6). This being so, one would expect the tendency to lay clutches of 4 to be eliminated by natural selection, whereas in fact it is common. One possibility that may be kept in mind is that it may be advantageous to have a somewhat variable clutch-size, particularly as feeding conditions are not identical from one year to another.

Finally it should be noted that the Starling was selected for this first paper because the results are clear-cut. This is attributable to the possibility that, in this species, the only important non-hereditary modifications in clutch-size are largely sorted out by date of laying. The survival data for other species, treated in later papers, are not so clear-cut. The present data should also be compared with those already published for the Alpine Swift (*Apus melba*), in which the basic problem is the same, and a parallel answer has been obtained. The details, however, are very different, as in Swifts undernourishment of the nestling causes death in the nest, instead of afterwards (Lack and Arn, 1947).

Summary

1. In the European Starling (*Sturnus vulgaris*) the clutch varies from 1–10 eggs. The average size of clutch and brood is smaller in late than early broods, and smaller in England than in Switzerland (tables 1 and 2).

2. Each nestling is fed less often in a brood of large than one of small size (table 3), and the few data on nestling weights support this view (table 5).

3. The percentage of eggs which produce fledged young is closely similar for broods of all the ordinary sizes found in nature (table 4).

4. Among Starlings which survive at least three months after leaving the nest, the recovery-rate is lower for young from broods of above average size than it is for young from broods of average size or smaller (tables 6, 8 and 10). Correspondingly, for Starlings dying within two months of leaving the nest, the recovery rate is higher for young from broods above average size than for young from broods of smaller size (tables 7 and 9). These differences hold for both early and late broods, and for Switzerland, Britain, and Holland. In only two cases are the differences statistically significant, but all of the seven possible analyses give concordant answers.

5. These results imply that, in the first two months after leaving the nest, the mortality-rate is higher among the young from broods of large than small size. As a result, broods with one or two more young than the average give rise to about the same number of descendants as broods of average size, i.e., broods of these sizes are about equally efficient.

6. The smaller size of late than first clutches, and of British than Swiss clutches, is considered to be advantageous, since in each case the mortality-rate rises as soon as brood-size exceeds the commonest size found in nature.

7. Annual differences in average clutch-size are small (table 11). Had there been extensive non-genetic modifications, the apparent rise in mortality-rate with brood-size would have been obscured.

8. Each individual tends to lay a clutch of similar (but not necessarily identical) size in different years (Appendix I).

9. Two individuals from the same brood are recovered rather more frequently than would be expected by chance (table 12).

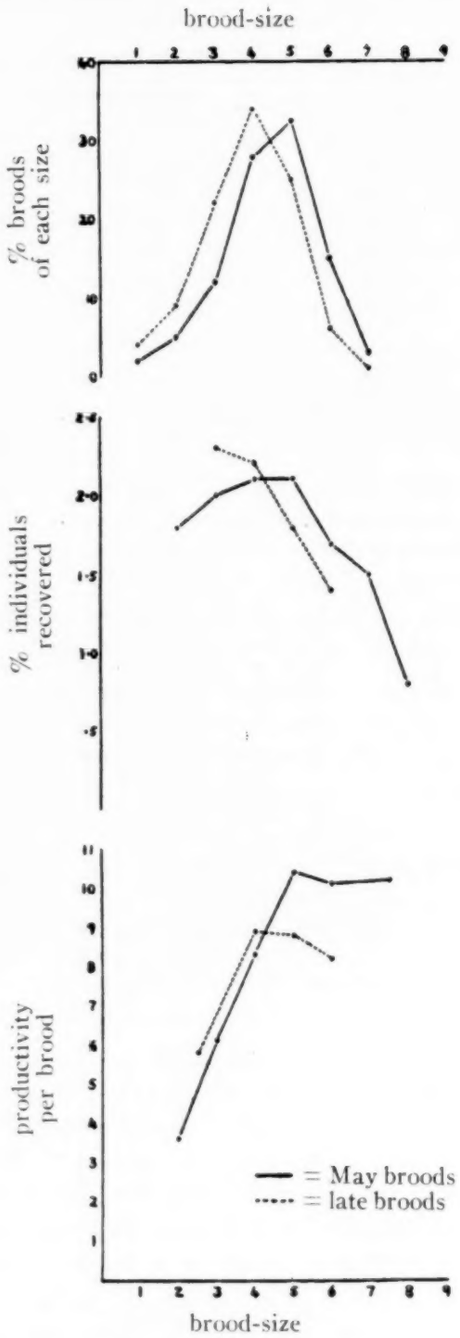

Fig. 1. Brood-Size and Survival in Swiss Starlings Based on Data in Table 6.

10. Swiss Starlings appear to have a higher average annual mortality-rate than British Starlings (table 13). This is an inevitable consequence of the higher reproductive rate of the former.

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APPENDIX I. *Successive layings of same female in different years (H. N. Kluijver)*

	A. In three successive years			B. In two successive years	
	1932	1933	1934	Layings of	No. of cases
(i)	6	6	6	3 and 6	1
(ii)	6	6	6	4 and 5	2
(iii)	6	6	6	4 and 6	2
(iv)	6	7	6	5 and 5	3
(v)	6	7	7	5 and 6	5
(vi)	7	7	8	6 and 6	10
				6 and 7	1

Notes: (i) Late layings, and layings known to be due to first-year birds have been omitted, but some of the latter may have been included inadvertently.

(ii) In Part B, the smaller laying did not necessarily come in the earlier of the two years.

Appendix II. Annual Differences in Survival

An analysis of survival-rates in each year separately did not yield results of interest. However, as this point is important in other species, the data are set out below for May broods in Switzerland for those years with a large number of recoveries. For other years in Switzerland, for all late broods, and for all British data, the recoveries were too few for this to be worth while.

Annual differences for May broods in Switzerland

Brood-size	No. of young banded in					No. of young recovered in				
	1933	1934	1935	1936	1937	1933	1934	1935	1936	1937
1	9	6	10	8	7	—	—	—	—	—
2	52	28	62	36	44	1	1	—	—	1
3	153	171	183	147	174	1	7	3	1	3
4	460	500	644	496	548	11	8	15	14	8
5	820	695	1240	645	795	24	21	30	13	8
6	432	324	534	258	444	9	6	5	7	4
7	49	98	112	63	77	1	1	1	1	1
8–10	8	16	49	27	8	—	—	—	—	1
Total	1983	1838	2834	1680	2097	47	44	54	36	26

VARIATION AND HYBRIDIZATION AMONG THE PARADISE FLYCATCHERS OF AFRICA

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INTRODUCTION

One of the differences between plants and animals, it is often stated, is the frequency of interspecific hybridism among plants, or its extreme rarity among animals. Such hybridism among animals has either been found in the zones where two allopatric forms meet, or else it has produced only occasional crosses between sympatric species. Familiar examples of the first class are furnished by the American flickers (*Colaptes auratus* and *cafer*) and the crows of Europe (*Corvus corone* and *cornix*). The second class is illustrated by the hybrids among ducks and birds of paradise, to mention only two groups.

Hybrid "swarms" resulting from the breakdown of isolating mechanisms between sympatric species are rare among animals, though known in the genera *Bufo* and *Colias*. Among plants, where such occurrences appear to be much more frequent, the hybrids may plainly affect the appearance of one or both parental species by backcrossing. Such penetration of genes from one species into another, without either losing its identity, has been called "introgressive hybridization" by Edgar Anderson. A summary of known cases among plants has been prepared by Heiser (in press). The present paper is devoted to a discussion of several cases of introgressive hybridization between sympatric species of a genus of birds.

THE GENUS *Terpsiphone*

The paradise flycatchers, composing the genus *Terpsiphone*, are now referred to about eleven species, which are distributed all the way from the western and southern extremities of Africa to Japan, the Philippines, and the Lesser Sunda Islands (Flores and Sumba). They are often crested, and adult males frequently grow two long median tail-quills, but certain species and races do not share those characters. Conspicuous polymorphism is exhibited by the adult males of *Terpsiphone paradisi*, *viridis*, and *mutata*. Some retain a rufous coloration on the back, rather like that of females, while others acquire white backs, and the tail then usually becomes mainly white. But in some cases the back becomes black, with or without a corresponding change of tail-color. The rufous males of some races of *T. paradisi* have glossy black throats, of others the males remain gray-throated. Rufous males of *T. mutata* are reddish on throat and breast, but have white on wing-coverts, and may grow white median rectrices. *T. viridis* over a large part of its range has no white on back, wing-coverts, or tail; but in the remaining regions it usually shows some white on the wing, and over much of the same area white-backed males are frequent. Mixed coloration on the back, rufous-and-white, rufous-and-gray, or even black, is frequently seen in parts of tropical Africa.

Thus the adult males in some populations of *paradisi* have two color phases, one of which is rare or lacking in certain regions; those of *mutata* on the island of Madagascar have been said to exhibit four; and those of *viridis* in some parts of equatorial Africa are so variable that one is a little puzzled as to whether there

are three, or four, or even more distinct types of plumage.

The geographic distribution of these color phases may help somewhat in the recognition of subspecies; fortunately there are usually other differences in size, proportions, and pigmentation. The group of species with crests and tails well developed includes *mutata, corvina, viridis, atrochalybeia, paradisi,* and *atrocaudata.* The forms which have the males most consistently black are apt to be found on oceanic islands. The species in which the tail-feathers are least apt to be prolonged are *T. bourbonnensis* (Mascarene Islands), *T. cyanescens* (Palawan), *T. cinnamomea* (Luzon and other islands in the Philippines), and *T. rufiventer* (tropical Africa). *Terpsiphone rufocinerea* of equatorial Africa has one race without elongated rectrices. Among these five species the crest is fairly well marked only in *bourbonnensis* and *cyanescens;* it is reduced or wanting in the others.

Except in tropical Africa there seem never to be two species breeding in the same area, although the paradise flycatchers of China and Japan migrate southward in the autumn and invade the homes of other forms. In the forested regions of Upper and Lower Guinea, however, two and often three species occupy the same area throughout the year. This provides an opportunity for hybridism that is lacking elsewhere.

The accepted number of African species has been greatly reduced in recent years. In 1903 Reichenow listed eleven from that continent; in 1930 Sclater still admitted eight. But in 1924 Stresemann had already brought the figure down to three, although for a short time afterward he was

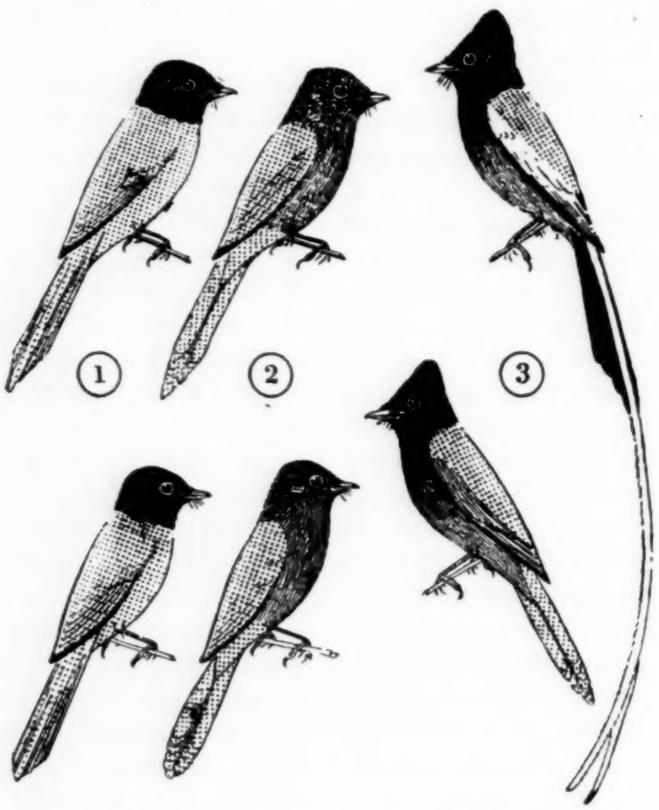

FIG. 1. Three species of *Terpsiphone* living together in the forest area of the northeastern Congo: 1, *T. rufiventer ignea;* 2, *T. rufocinerea batesi;* 3, *T. viridis speciosa.* In the upper row are the adult males; in the lower, females.

On these and the following sketches the dotted areas are rufous, and parallel shading indicates gray.

not sure there might not be a fourth, *plumbeiceps*. Then it became clear that *plumbeiceps* was only a race of *T. viridis*, and that it migrated during the dry season into equatorial regions where the resident population belonged to other races. In my opinion, most of Stresemann's conclusions are well supported by the field studies that have been carried out since 1924, except with regard to hybridism.

Geographic Variation and Polymorphism in Continental Africa

When I began collecting paradise flycatchers in the Ituri Forest, in the northeastern Belgian Congo, in 1909, it was clear that I was dealing there with three quite distinct species (fig. 1). *Terpsiphone viridis*, with well-developed crest in both sexes, black-and-gray underparts and elongated median rectrices in all adult males, was common amid trees in clearings and second-growth woods, but not to be seen in primary forest. The untouched forest held two other species: one with gray underparts, rufous under tail-coverts, no long tail-quills, and the crest only slightly developed (*T. rufocinerea*); the other with breast rufous, but throat black or gray, little lengthening of median rectrices, and no crest (*T. rufiventer*).

So far as I could see, the species *rufocinerea* and *rufiventer* in the Ituri lived in exactly the same places and in the same fashion, moving actively about in the rather open undergrowth. Both seemed to join frequently in the mixed parties of small insectivorous birds that are so characteristic. Their call-notes seemed alike, nor did these differ appreciably from the call of *T. viridis*.

The two species of the deep forest, about Avakubi and Medje, showed no polymorphic plumages. Adult males of *Terpsiphone viridis* in the central Ituri were usually rufous on the back, with considerable white on the wings, and with two long white rectrices. But white-backed males of *viridis* are not rare in many forested parts of the Upper Congo; and some

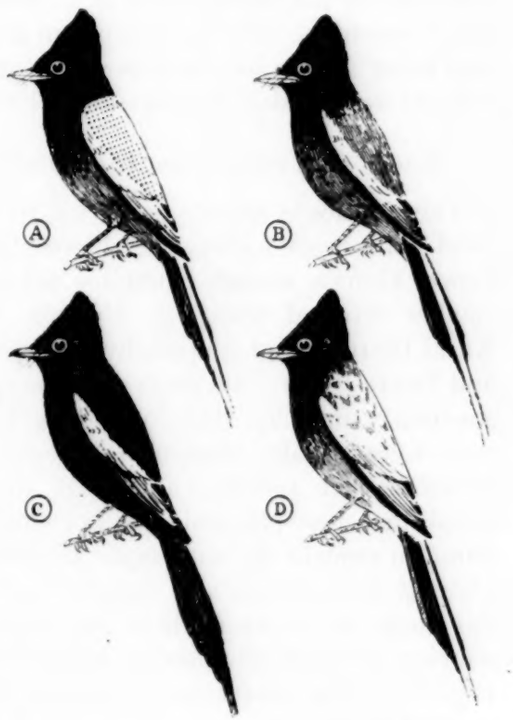

Fig. 2. The four principal color phases of *Terpsiphone viridis speciosa* found in the forest area of the Upper Congo: A, rufous-backed with white on wings; B, gray-backed with white on wings; C, black-backed; and D, white-backed. Rufous coloration is indicated by dotted pattern.

adults of that sex become almost wholly black on the back, with the long rectrices mainly black. Thus one might say that there are four color phases (fig. 2), though the distinction between rufous-backed and black-backed birds is not very sharp. Males in which there is an admixture of gray or black to the rufous of the back may tend to bridge the gap. Gray-backed males also occur. Females are all alike, rufous-backed, without white on wings or tail.

If we start from this central region and follow the three species out toward the periphery of their ranges, we find their geographic variation quite diverse. This gives support to the specific status accorded to *viridis*, *rufocinerea*, and *rufiventer*. Yet there are a few areas, as we shall see, where their characters seem to undergo perplexing recombinations. In Africa only *T. viridis* normally exhibits

color phases paralleling those of *T. mutata* and *T. paradisi*. The polymorphism of the two latter species has been carefully studied and described by Salomonsen (1933).

Races of *Terpsiphone rufiventer*

This species is mainly restricted to the solid rain-forest areas of Upper and Lower Guinea, though extending out into smaller wooded areas in Uganda, the Kasai District, and supposedly in Nigeria and Sierra Leone. Its races differ so conspicuously in color that for a long time they were usually thought to belong to three distinct species; and it is to be noted that few physical barriers can be found to explain the subspecific variation. Only at the western and eastern ends of the range do crown-feathers and median rectrices undergo any marked lengthening (fig. 3). The subspecies commonly recognized at present are:

1. *T. rufiventer rufiventer* Swainson. Gambia and Portuguese Guinea. Largely rufous, with black head well crested, some white on wing-coverts, median rectrices long and rufous.

2. *T. rufiventer nigriceps* Hartlaub. Sierra Leone to Gold Coast. Largely rufous, head black without crest, no white on wing, median rectrices not greatly lengthened.

3. *T. rufiventer fagani* Bannerman. Southern Nigeria. Like *nigriceps*, but browner, especially on back.

4. *T. rufiventer tricolor* Fraser. Fernando Po. Bluish gray on back, wings, and tail; head black without crest; throat black or gray, breast rufous; tail-feathers not lengthened.

5. *T. rufiventer neumanni* Stresemann. Niger Delta, Cameroon, and Gaboon. Like *tricolor* in color, slightly smaller.

6. *T. rufiventer smithii* Fraser. Island of Annobon in the Gulf of Guinea. Rufous with black head, not crested, remiges and rectrices bordered with gray.

7. *T. rufiventer mayombe* Chapin. French Congo and Mayombe to Eala on the middle Congo River. Very like *smithii*, but perhaps deeper rufous on body and more bluish gray on wings and tail.

8. *T. rufiventer schubotzi* Reichenow. From Yokadouma in the Cameroon to Bangui on the Ubangi River. Like *mayombe*, but head gray, in both sexes, never becoming black in males.

9. *T. rufiventer bedfordi* Ogilvie-Grant. Northeastern Ituri Forest. Entirely bluish gray except on head, which is blackish, without crest. Rectrices little lengthened.

10. *T. rufiventer ignea* Reichenow. Northern edge of Angola to the Upper Congo and Ituri. Like *mayombe*, but duller and browner on remiges and rectrices. Head of adults becomes black, but never crested.

11. ***T. rufiventer somereni*, new subspecies.**

This race is rather similar to *ignea*, but differs by the more reddish, less brownish color of all its retrices and its inner secondaries. From *emini* it differs in lacking any crest, having the black area on throat less extensive, the body-color lighter rufous, and the median rectrices of males seldom prolonged more than 35 mm. Thirty specimens have been examined.

Type: Am. Mus. Nat. Hist. No. 652,518, ♂ adult, Budongo Forest, Uganda, June 14, 1919, collected by V. G. L. van Someren. Wing 78 mm.; median tail-quills 116, next-longest 83; culmen to base 19.

Range: Bugoma and Budongo forests in Bunyoro Province of Uganda, southeastward to those in Kyagwe.

It must also be noted that *somereni* bears a marked resemblance to *nigriceps* of Upper Guinea, though its body-color is normally not quite so deep rufous. This difference is particularly well marked in the more easterly part of the range of *somereni*, near the Sezibwa River and the Mabira Forest.

12. *T. rufiventer emini* Reichenow. Uganda (except north), lower Kagera Valley, Kavirondo District. Typically rufous, with crested head black, tail rufous, its median quills usually prolonged in males.

Races of *Terpsiphone rufocinerea*

Mainly confined to forest regions in Lower Guinea, this species looks more like *T. viridis* than *T. rufiventer*. It is not polymorphic and its races do not show any great diversity in color.

1. *T. rufocinerea rufocinerea* Cabanis. Lower Congo, Gaboon, and western Cameroon. Head of male blackish, without marked crest; back, wings and tail rufous; median rectrices of males usually rather long.

2. *T. rufocinerea batesi* Chapin. Interior of the Cameroon eastward to the Ituri District. Head gray, crest short, colors lighter than nominate race, and tail not lengthened.

3. *T. rufocinerea bannermani* Chapin. More wooded parts of northwestern Angola. Grayer about head and breast than the nominate form, but with lengthened rectrices in adult males; crest slightly developed (fig. 4).

FIG. 3. Some of the races of *Terpsiphone rufiventer*: 1, *rufiventer*; 2, *nigriceps*; 3, *neumanni*; 4, *mayombe*; 5, *ignea*; 6, *bedfordi*; 7, *emini*.

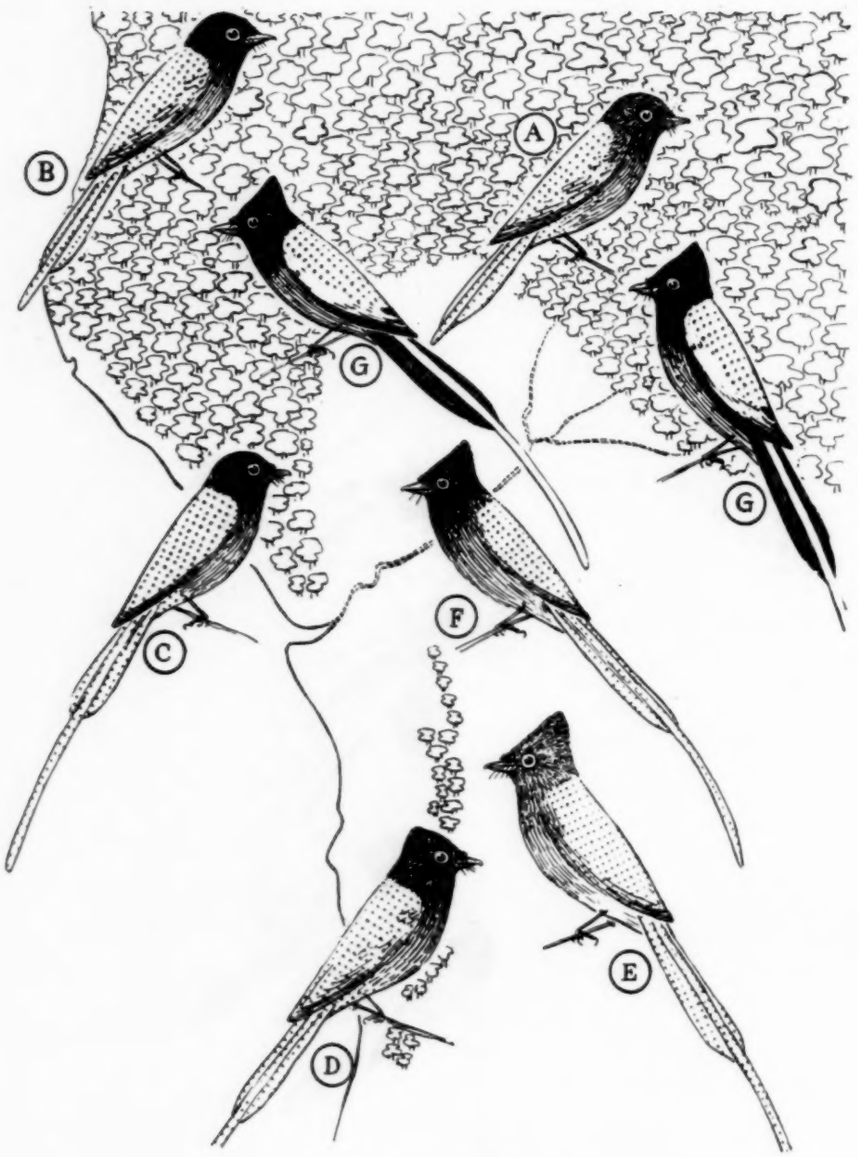

FIG. 4. Diagram to explain hybridism between *Terpsiphone rufocinerea* (A–D) and *T. viridis* (E–G). A, *T. r. batesi* of Upper Congo; B and C, *T. r. rufocinerea* of coastal area from Cameroon to Congo; D, *T. r. bannermani* of northwestern Angola; E, *T. v. plumbeiceps;* F, *T. v. "melampyra"* of Lower Congo; G, *T. v. speciosa* of Cameroon, Gaboon, and Upper Congo (rufous-backed phase).

RACES OF *Terpsiphone viridis*

The exact number of subspecies to be recognized in this group is still a matter for debate, largely because of polymorphism over large areas (Fig. 2). A fair appraisal at the present time is as follows:

1. *T. viridis viridis* P. Müller. Lower Senegal eastward perhaps to Nigeria. In birds from Senegal the breast is very glossy black, under tail-coverts rufous, wing with considerable white; but white-backed males are unknown there. The white-backed phase appears near the upper Niger River and in southern Nigeria.

2. *T. viridis ferreti* Guérin. Southwestern Arabia, Eritrea, Somaliland, and Abyssinia, westward across the Sudan to Lake Chad or beyond, southward to the Bahr-el-Ghazal, Uganda, and the East Coast near Tanga. White-backed males are lacking or rare in Arabia and northern Abyssinia, but elsewhere usually common. On the eastern coast they predominate.

3. *T. viridis speciosa Cassin.* Cameroon, Gaboon, forested area of Upper Congo and Kasai; eastern limit in Semliki Valley and Manyema District. Males usually assume long white median rectrices, but outer tail-feathers generally remain blackish, and whole tail may be mostly black. Their backs may be rufous, rufous-and-gray, gray, white, or black.

4. *T. viridis suahelica* Reichenow. Highlands of Eastern Africa from Kikuyu and Mau to Kilimanjaro. Males have only a rufous phase, but normally assume some white on wing-coverts, none on tail.

5. *T. viridis restricta* Salomonsen. Islands in Lake Victoria, especially the Sesse Islands and Nkose. Very black on breast, with rufous under tail-coverts; like *T. v. viridis*, but long median rectrices often white.

6. *T. viridis ruwenzoriae* Grant and Mackworth-Praed. From southwestern Uganda and eastern edge of the Upper Congo Forest eastward to northwest Tanganyika Territory. No white on back, wings or tail; head rather black and glossy; under tail-coverts rufous.

7. *T. viridis ungujaensis* Grant and Mackworth-Praed. Usambara highlands, Zanzibar Island, and adjacent coastal area of Tanganyika Territory. Like *ruwenzoriae* but belly and under tail-coverts whitish.

8. *T. viridis perspicillata* Swainson. Southeastern Transvaal and Zululand to Cape Province. Like *ungujaensis* in color, but slightly larger.

9. *T. viridis violacea* Grant and Mackworth-Praed. Nyasaland and perhaps some adjacent regions in Tanganyika Territory and the southeastern Congo. Intermediate in color between *ungujaensis* and *plumbeiceps;* i.e., close to *plumbeiceps* but a little more blackish and glossy on crown. (May migrate northward in off-season to Lake Albert and the East Coast near Mombasa.)

10. *T. viridis plumbeiceps* Reichenow. Breeding from Southwest Africa and Angola to the Katanga; migrates northward in off-season to the forested Cameroon and Uelle District of northeastern Congo. It has frequently been found in the range of *T. v. speciosa*, mainly from April to October, but has never been known to nest there.

Interspecific Hybridism in Africa

It goes almost without saying that along the boundaries between the various races of each species, certain individuals are found that show signs of intergradation or interbreeding between the races. In some cases the transition zone, as between *Terpsiphone rufiventer bedfordi* and *T. rufiventer ignea*, may be surprisingly narrow.

Much more remarkable is the fact that in three quite separate parts of tropical Africa there are considerable populations of *Terpsiphone* which offer every evidence of having arisen by hybridization between two of the three species already discussed. The outstanding characters which usually distinguish these species are:

(1) the length of the crown-feathers (whether or not they form a well-marked crest);

(2) prolongation of the median pair of rectrices in adult males (or lack of any appreciable lengthening);

(3) color of breast and flanks (whether blackish, gray, or rufous);

(4) sharply marked color change between throat and chest (or a gradual transition from black or gray throat to gray breast); and

(5) the presence or absence of a white-backed phase among adult males.

In a few cases certain of these features may seem to vary geographically within a species. But when, within a relatively short distance, we find not only two plainly distinct species, but also numerous examples exhibiting intergradations between them, or a recombination of some of the differential characters listed above, then I feel that we are confronted with true hybrids.

It seems best to take up first a very simple case, an exceptional hybrid between the two species living in heavy forest, and then to go on to the cases of hybrid populations in border regions of the Guinean forests.

(1) *Terpsiphone rufiventer* × *rufocinerea*

Although these two species are so commonly associated in the heavy forests of the Cameroon, Gaboon, and Congo, hybridization between them is all but unknown. Yet I can cite one indisputable case. An adult male *Terpsiphone*, col-

lected for the Carnegie Museum by J. A. Reis, Jr., in September 1924 at Ntuleñ, between Sakbayeme and Yaunde, Cameroon, puzzled me for years. I could not decide whether to refer it to *T. rufiventer* or to *T. rufocinerea*. Although found within the range of *T. rufiventer neumanni*, it had a rufous, not a gray back. Its head was gray, suggesting *T. rufocinerea batesi*, yet it had wings and tail much more like those of *T. rufiventer schubotzi* and *mayombe*, the outer edges of the primaries and the distal parts of the rectrices bluish gray. The gray of the throat was continued down on the chest, but then turned rapidly to whitish, lightly washed with rufous-buff on lower breast, abdomen, and flanks.

This bird has no resemblance to *T. viridis*, its crown feathers and median rectrices are no more elongated than those of *T. rufocinerea batesi*, which I should regard as one of the parents. The color of wings and tail convinced me of its *rufiventer* heritage, as well; and if the back has no trace of the gray of *neumanni*, we may conclude that the genes which produce the red back-color in *rufocinerea* have somehow been dominant over the gray color seen in *neumanni*.

Much more difficult to explain is the whitish color of the posterior under surface, and on that subject I have nothing to suggest. At Boma on the lower Congo River I once shot an immature example of *T. r. rufocinerea* with whitish breast, but can think of no good reason for such exceptional coloration. The type of *T. camburni* is likewise only an immature *bedfordi* with whitish breast.

(2) *Terpsiphone rufocinerea* × *viridis*

In northwestern Angola, at Ndala Tando, Canhoca, and Ngara near Novo Redondo, one finds what appears to be a population resembling *T. r. rufocinerea* in color pattern, even to the rufous under tail-coverts, but notably lighter, especially on head and throat. In this respect they seem intermediate between nominate *rufocinerea* and *T. viridis plumbeiceps*. David Bannerman (1936) called attention to these paler examples of *rufocinerea* from Ndala Tando, and in the few skins I have had for examination I find that the crest-feathers are intermediate in length between those of *T. r. rufocinerea* and those of the relatively long-crested *T. v. plumbeiceps*. It has seemed best to distinguish this population as *Terpsiphone rufocinerea bannermani*, even though its characters are due to hybridism (fig. 4).

Undoubted specimens of *plumbeiceps* have also been collected at many localities in that same section of Angola; and it seems probable that both forms breed there, the more deeply colored birds with bright rufous under tail coverts being restricted to the areas that are most heavily wooded. The range of *plumbeiceps* extends far to the southward, and this race is known to have a regular migration which extends in the off-season north to the forest of the Cameroon. Inasmuch as *T. v. plumbeiceps* never has any white on back, wings, or tail, and both the supposed parent forms have no sharp change of color between throat and chest, it seems natural for their mixed offspring to be rather uniform in coloration. If we did not know that in the Cameroon-Congo forests *T. viridis* and *rufocinerea* behave as valid species, we should be inclined to treat *T. r. bannermani* as conspecific with *plumbeiceps*, and to regard these birds of wooded localities in northwestern Angola as mere intergrades between geographic races.

(3) *Terpsiphone viridis* × *rufiventer*, in West Africa

Another region in which a population seems to have developed from interbreeding, this time of *T. viridis* with the species *rufiventer*, is that of the Gambia River and Portuguese Guinea. The result of this combination I have treated as the nominate race of a species, because it was from a member of this population that *rufiventer* was described by Swainson in 1837, before most of its near relatives were known (fig. 3).

Nearly all the other geographic representatives of *T. rufiventer* have no greatly lengthened rectrices, and no white on the wing. They range from Sierra Leone to Uganda. Nominate *rufiventer* is exceptional in having a well-developed crest, as well as lengthened middle tail-feathers and a variable amount of white on the wings of adult males. These are features found frequently in *T. viridis*. But the throat of *T. r. rufiventer* is black, the breast rufous, whereas in *T. v. viridis* both throat and breast are blackish. Here we have an unusual combination of characters.

To me it seems evident that such a combination would naturally result if *T. v. viridis* of Senegal were crossed with a bird like *T. rufiventer nigriceps* of Sierra Leone. The two supposed parent forms can still be found near each other in Sierra Leone, and possibly in French Guinea. Specimens of *T. r. rufiventer* are not numerous in museums. Here in the United States I have located but two, in the Museum of Comparative Zoölogy. The British Museum is reported to have about thirteen, and these have been examined for me by my friends Bannerman and Moreau. They find some variation in the amount of white on the wing; and while the black of the throat is usually cut off sharply from the rufous chest, there are a few skins where the black extends to the middle of the chest, or where the rufous chest-feathers are margined distally with black. After examining a smaller series in Berlin, Stresemann (in litt.) now agrees that hybridization is the best explanation.

These variants offer convincing proof of the hybrid origin of *rufiventer*. The question that immediately arises concerns Sierra Leone. Both parent forms are found there, but why no hybrids? It would seem that the more heavily wooded a country is, the less likely this process of hybridization. Observations on breeding pairs in Portuguese Guinea would be most desirable.

(4) *Terpsiphone viridis* × *rufiventer*, in Uganda

A second area where similar interbreeding between the same two species, though represented by other races, must have occurred lies in the region of Lake Victoria, from Bukoba on its western shore around to Entebbe and Mabira on the north, and even to the North Kavirondo District in the east. The variability of paradise flycatchers in that region is celebrated in ornithological literature (fig. 5).

We may begin by discussing the probable parent stocks. In the greater part of Uganda, *Terpsiphone viridis ferreti* is common. The males exhibit two color phases, one with rufous back and some white on the wings, the other with white back, wing-coverts, and tail. In southwestern Uganda all white on wings or tail is lost, and the resident race is *T. v. ruwenzoriae*, with no white-backed phase. The Sesse Islands race, *T. v. restricta*, has little or no importance in this connection.

The representative of *T. rufiventer* in the Bugoma, Budongo, and Mabira forests is *T. r. somereni*, a rufous bird with blue-black head, differing from *ignea* of the eastern Congo Forest by having wings and tail more reddish. The tail usually shows little elongation of its median quills. Such birds are restricted to the denser woodlands.

In addition to these two well-marked species we find birds in Uganda which have long puzzled ornithologists. Now it becomes evident that they are the product of hybridization between *T. viridis* and *T. rufiventer*. Foremost among them is the form described by Reichenow in 1893 as *Terpsiphone emini* from Bukoba. It has often been considered a valid species; the crest is well developed, head and throat are glossy black, the breast rufous. Wings and tail are rufous, median rectrices well lengthened. In some ways *emini* is like *T. r. rufiventer*, and rarely has it a trace of white on the wing. This last character may be explained by the

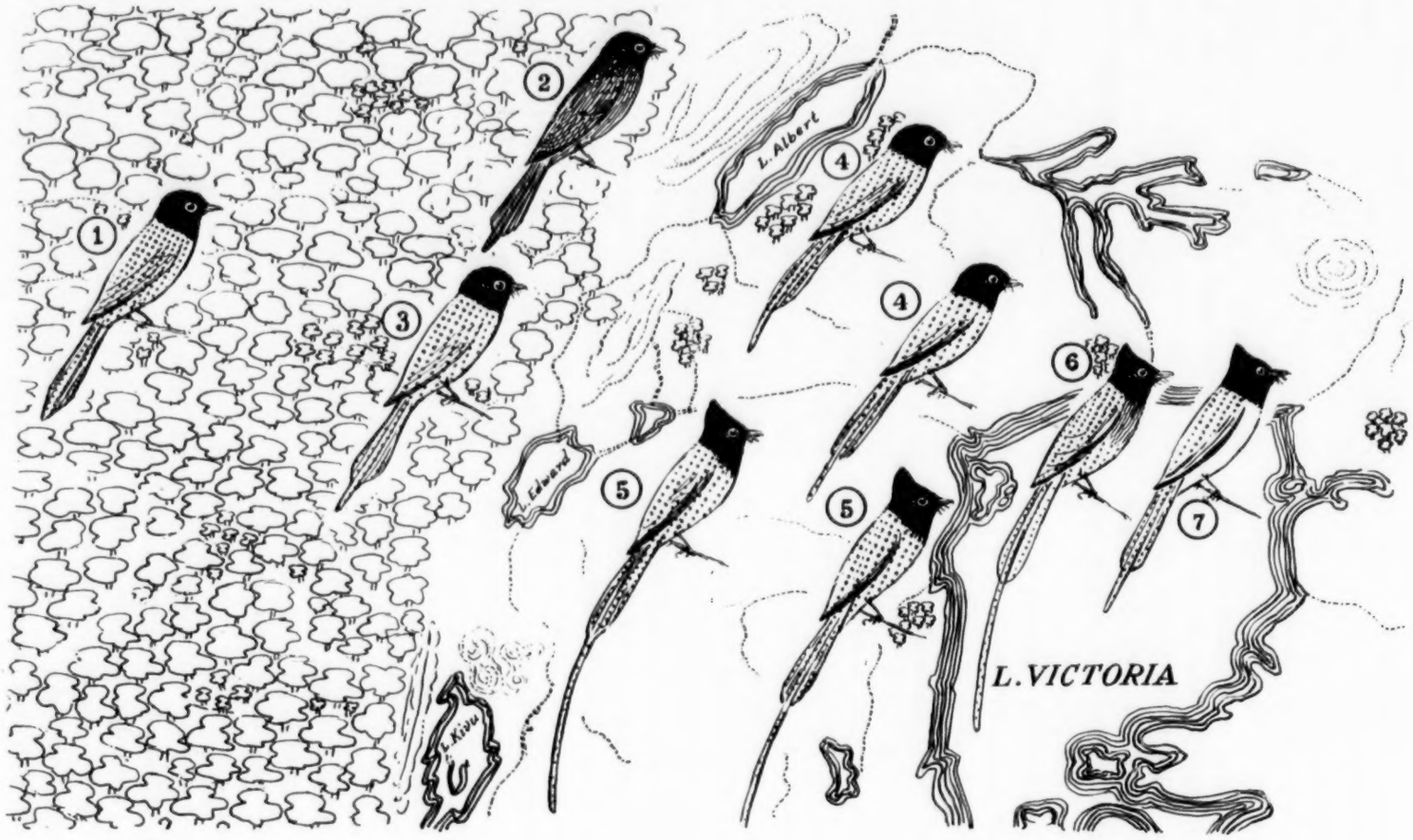

FIG. 5. Races of *Terpsiphone rufiventer* in the eastern Congo and Uganda, and the principal hybrid forms found in Uganda. 1, *ignea*; 2, *bedfordi*; 3, *ignea* × *somereni*; 4, *somereni*; 5, *emini*; 6, "*poliothorax*" hybrid; 7, "*albiventer*" hybrid. Various races of *Terpsiphone viridis* range virtually throughout the area.

fact that in southwestern Uganda *T. viridis* is represented by the race *ruwenzoriae*, with no white on wings or tail. Indeed if one tries to imagine the result of crossing *T. v. ruwenzoriae* with *T. rufiventer somereni*, it must be a bird very like *emini*.

Here and there, to the west and north of Lake Victoria, other paradise flycatchers have been found of still different appearance. When Reichenow in 1916 described *T. poliothorax* from Bukoba, he remarked that this bird might prove to be a hybrid between *emini*, which he still thought a distinct species, and *T. viridis*. The type of *poliothorax* was rufous on the abdomen and flanks, gray on the middle of the breast, and the gray shaded gradually into the black of the throat. Other specimens of "*poliothorax*" coloration have since been obtained along the northern side of Lake Victoria, but it is clear that they do not constitute a population, much less a species.

A limited number of males, still more remarkable in color, have been secured at localities extending from Kakamega on the east to Budongo on the west. These have the head and throat glossy black, a moderate crest, rufous backs, breast and abdomen largely white. Such birds, no doubt, prompted van Someren (1922) to say that "undoubted hybrids between *T. emini* and *ferreti* occur!" Yet thus far almost everyone continued to regard *emini* as a species. In 1925 Stoneham described one of these white-breasted males from Bombo, Uganda, as *Tchitrea albiventris*, plainly not a valid species. In 1924 Stresemann had already discussed such white-breasted individuals as the "*albiventer*-variant" of *emini*, which he listed among the races of *T. rufiventer*. Sclater in 1930 admitted that *poliothorax* might be a hybrid, and listed *emini* as a race of *T. nigriceps*. Van Someren in 1932 again insisted that *emini* undoubtedly crosses with *viridis*, and concluded that "*albiventris*" was one of the hybrids.

With regard to hybridism in Uganda, I am satisfied that van Someren was amply justified in his conclusions; but he did not go far enough, for *emini* itself is very plainly a hybrid population or race. Since it has, in the main, the color-pattern of the *rufiventer* group, we shall do well to follow Stresemann in treating it as a subspecies of *T. rufiventer*. Yet as more material becomes available, *emini* is clearly connected with *T. viridis ferreti* and *suahelica* by a whole chain of intermediates—the hybrids to which van Someren pointed. The actual composition of some of the hybrid populations is recorded in table 1.

A geographical tabulation of specimens of *Terpsiphone* examined during the preparation of this paper, with the addition of the published figures for "*poliothorax* and "*albiventris*" accompanying the original descriptions of those

TABLE 1. *Observed frequency of various forms of* Terpsiphone *in four areas in and near Uganda*

	Budongo-Bugoma area	Entebbe-Mabira area	Bukoba-Kagera area	North Kavirondo area
T. rufiventer somereni	9♂, 7♀, 6 yg	3♂, 7♀, 3 yg	0	0
"*emini*"	0	2♂, 1♀, 1 yg	2♂, 2 yg	2♂
"*poliothorax*"	1 yg	2♀, 1 yg	2♂, 1♀ (type series)	2♂
"*albiventer*"	1♂	1♂ (type of *albiventris*)	1 yg	1♂
T. viridis ferreti	7♂ w-b 6♂ r-b 2 yg	5♂ w-b	0	4♂ w-b 2♂ r-b 2♀, 2 yg
T. viridis ruwenzoriae	0	0	1♂, 2♀, 4 yg	0

yg = young. w-b = white-backed. r-b = rufous-backed.

forms. I wish to thank Dr. V. G. L. van Someren for the loan of eight specimens included in this table.

It will be noted that in the Budongo-Bugoma area, nearest the Congo, *T. rufiventer somereni* and *T. viridis ferreti* are both numerous, and hybrids rare. In the Entebbe-Mabira area both parent species are still common, but the hybrids more numerous. The Bukoba-Kagera area (southernmost) and the North Kavirondo area (the easternmost) both lack the *rufiventer* parent, though three kinds of hybrids have been collected in each. Minor peculiarities of the hybrid specimens have necessarily been ignored in the tabulation. In the Bukoba-Kagera area *T. viridis* is represented by the race *ruwenzoriae*, in other areas by *ferreti*.

Why the underparts should become white in a small proportion of the hybrids in the Uganda region is difficult to say. But it is to be noted that most or all such specimens have been taken in localities where white-backed males of *T. viridis ferreti* are common.

Ecological Interpretation

Most students of *Terpsiphone* thus far have invoked polymorphism, rather than hybridism, to explain all the complex variants that are so familiar in tropical Africa. Stresemann (1924) provided the best arrangement of African species and races; yet after reducing the number of species to three he was unwilling to admit any likelihood of hybridization between those species, even in Uganda.

Of the prevalence of polymorphism there can be no doubt. The male color phases of *T. v. speciosa* and of *T. v. ferreti* are clear-cut examples. The areas where such conditions prevail are broad and fairly well defined. In the species *T. rufiventer* the plumage color shows decided uniformity in any one place, but the geographic races differ from one another in ways that suggest conspicuous mutations. The back is bluish gray in *T. r. tricolor*, *T. r. neumanni*, and *T. r. bedfordi*, but rufous in most other races. Even the breast is bluish gray in *bedfordi*, so that the whole plumage lacks rufous, and a normal example of that form recalls a "melanistic" or deep gray mutant of the crested *T. viridis ruwenzoriae* which van Someren has lent me from southwestern Ankole.

These color-mutations seem not to be correlated with the development of the crown-feathers, and seldom does the length of the median rectrices show any great diversity in fully adult males, except in certain definite areas along the borders of the great rain forest inhabited by *T. rufiventer* and *T. rufocinerea*. These areas of exceptional variability are of relatively small extent, and the variability there exhibited is so great as virtually to bridge the gap between two of the species which dwell in those regions. One of the species seems to keep more to patches of forest, the other more to grasslands with many trees. A treeless plain would not attract any *Terpsiphone*.

While admitting the great tendency to variability of color in both *viridis* and *rufiventer*, I regard interspecific hybridism as the only sufficient explanation for the existence of the populations which we call *T. r. rufiventer*, *T. rufiventer emini*, and *T. rufocinerea bannermani*. It might be argued that if these are all hybrids they should not be dignified with subspecific names. They usually live in the same areas as some form of *T. viridis*, which I regard as one parent form, and not far from a different, forest-dwelling form which I take to be the other parent stock. But the forest-dwelling parent, in each instance, seems to be on the decline.

Let us examine the conditions now prevailing in Uganda. I see no valid reason why mutation alone should provide more extreme variations there than in any neighboring part of the Belgian Congo. In the years to come I expect that a study of mated pairs in life will shed much additional light on the question. This should not be over-difficult, especially if the nest can be located, for the male is known to share in the duties of incubation. I venture to predict that mixed pairs will be found, especially near the edges of forest patches like those of Mabira. It will be

particularly interesting to see what types of females mate with the white breasted *"albiventer."*

After I brought this question to the attention of Captain C. R. S. Pitman in Uganda, he replied that during 1944–46 his garden in Kampala had been visited occasionally by a male bird of *"viridis"* type and a female of *"emini"* coloration. He did not find them nesting, nor could he prove they were mates. No male of *emini* was ever seen there, so the probability of their being a mixed pair seems very great.

The vegetational nature of the territory of each pair may well be important. From all I can learn from the labels of Uganda specimens, it seems that birds of *somereni* type are mainly restricted to the patches of heavy forest, from Bugoma and Budongo to Mabira. On the other hand, *Terpsiphone r. emini* seems to be content with smaller bits of woodland near the lake shore, and sometimes to frequent more open groves of trees. Birds of the *"poliothorax"* and *"albiventer"* coloration appear to occur in the sort of places that would suit both *emini* and *T. viridis ferreti*. In all the more open savannas, provided there are a fair number of large leafy trees, one certainly finds *T. v. ferreti* or *T. v. ruwenzoriae*. These representatives of *viridis* may be expected also to haunt the fringes of woods and to penetrate at times well into forest patches, particularly where there has been some chopping by man.

The belief is widespread and well founded that for centuries the rain-forest area of Africa has been shrinking, partly perhaps because of climatic changes, and to a large extent also because of human activities in clearing forest lands for agriculture and burning whatever high grass grows up along the borders of forests. This regrettable activity goes on, of course, on every edge of the equatorial forest belt, from Kavirondo and Uganda to Sierra Leone and French Guinea.

We have seen how the various races of *Terpsiphone rufiventer* with short crown-feathers and relatively short tails keep as much as possible in the shade of primary forest. Clear a few acres in the depths of the Ituri Forest in the Congo, and you will never see one example of *T. r. ignea* come out from the surrounding woods. But as shade trees and bushes grow up about your abode, *T. viridis speciosa* will make its appearance. In that country the true forest birds have no difficulty in avoiding the unwonted sunlight of your clearing.

At the eastern and western ends of the forest belt, however, conditions are very different. The forest has been broken up into isolated blocks. As these become smaller and smaller, the representatives of *T. rufiventer* which inhabit them are more and more encircled by distasteful grasslands. Refuge becomes increasingly difficult to find. At the same time the representatives of *T. viridis* are ever more apt to invade such small wooded areas, to come in close contact with the forest-dwelling species.

The call-notes of *viridis* and *rufiventer* are so similar that I never felt sure I could distinguish them—husky, bisyllabic, like "zrĕ-zrĕ." The song of *viridis* is an agreeable sequence of liquid whistles, three or four, all of about the same pitch. While I have never with certainty heard any such song from *T. rufiventer*, Bates (1930) has stated that it does have one of much the same type. Nests and eggs of both species are very much alike. These are facts that would reduce the obstacles to hybridization. I firmly believe that as some of the forest patches in and near Uganda approached the vanishing point, mixed pairs were certainly formed.

Along most of the long northern margin of the Congo-Cameroon forest belt this does not seem to have happened. As the forest border was gradually moved southward, the representatives of *T. rufiventer* could easily retreat into the kind of forest they craved. Any clearings or second growth available were used by *T. viridis*, but there I have seen no evidence of hybridism.

On the southern side of the Congo Forest there is at least one region where conditions parallel those in Uganda. The long strip of Mayombe Forest extends southward from the Gaboon almost to the lower Congo River near Boma. Between it and the coast is a strip of savanna, and to the east another large area of grassland. South of the Congo River other less continuous areas of woods string out into northwestern Angola, to Ndala Tando a little north of the Cuanza River, and even into the Amboim district, not far from Novo Redondo (fig. 4).

In this region, again, the wooded areas appear to have broken up into smaller and smaller patches. *Terpsiphone rufiventer* seems scarcely to extend south of the lower Congo River, and in the Mayombe Forest it is not known to interbreed with either of the other species. The other forest species, *T. rufocinerea,* however, is common in the Mayombe District, and there is blacker-headed and longer-tailed than in the Upper Congo Forest. As it extends southward into Angola, it comes to look more and more like *T. viridis plumbeiceps,* which also inhabits much the same region. Indeed, *T. rufocinerea bannermani* seems so nearly intermediate between *plumbeiceps* and nominate *rufocinerea* that here again hybridism offers the best explanation.

The case of *Terpsiphone r. rufiventer* in Portuguese Guinea and the Gambia is like that of *T. r. emini* in Uganda, though simpler. One supposed parent in forested Upper Guinea, *T. r. nigriceps,* is very like the race inhabiting the heaviest Uganda forests. But *T. v. viridis,* which must have been the other parent, shows few if any white-backed males in the region from Sierra Leone to Senegal. Its breast is blacker than that of *T. v. ferreti* or *T. v. ruwenzoriae.* Occasional specimens of *rufiventer* from West Africa show an extension of the black of the throat down on to the middle of the chest, much as gray runs down on the chest of "*poliothorax*" in Uganda. But males of nominate *rufiventer* usually have some white on the wing; *emini* rarely shows any. In the origin of *emini* the race *T. viridis ruwenzoriae,* with rufous wings, would seem to have played an important part.

It is certainly unusual for races of birds to arise by the interbreeding of valid species. Yet it would scarcely seem justifiable to reduce the three species of the Congo-Cameroon forest area to one, simply because somewhere else they can all be shown to intergrade. I prefer to argue that the three species *viridis, rufocinerea,* and *rufiventer* arose in the remote past by the usual process: isolated populations diverging as a result of mutation and selection. The barriers were perhaps differences or gaps in vegetational areas. One might argue that *viridis* is a relatively recent invader, showing greater resemblance to the Oriental *paradisi.* But such views are inadequate to account for races like *rufiventer, bannermani,* and *emini.* It seems much simpler to regard them as of recent origin, due not to isolation, but to the exact opposite, the breaking-up and destruction of forests, with interbreeding of species as a result.

An instructive comparison can be drawn from another group of birds, the drongo shrikes of the equatorial region of Africa. In all the heavy forests of Lower Guinea lives a form of *Dicrurus* called *coracinus,* with velvety black back and shining wings. It does not occupy the primary forest so much as it does the tall trees around the edges of clearings, but it is characteristic of heavily wooded areas and extends to suitable spots in Uganda and North Kavirondo. In the savannas on the north, east, and south of the Cameroon-Congo forest lives a related bird, of the species *D. adsimilis,* with the back glossier, much more like the wings. To those who know only these two in life, *adsimilis* and *coracinus* certainly seem like well-marked species. It was customary, to be sure, to treat *coracinus* as a race of the somewhat larger *D. modestus* of Principe Island in the Gulf of Guinea.

In forested Upper Guinea, from the Gold Coast to Sierra Leone, however,

there lives another form of the genus, *atactus*, which is exactly intermediate between *coracinus* and *adsimilis*, the latter bird occupying the savannas to the north. Careful study by Bates (1933) convinced him that *atactus* was a geographic race connecting *coracinus* of the Lower Guinea forest with *D. adsimilis* of the savannas of much of the African continent, so that all three forms must be regarded as conspecific.

Why then do *coracinus* and *adsimilis* seem so like species in the Congo? What keeps them from interbreeding there and in Uganda? In the main it would seem to be merely their strong preference for forest or for savannas. But here and there around the borders of the Lower Guinea forest there is actually some interbreeding, as Dr. Charles Vaurie has recently proved to me. He has shown me that specimens actually collected by me at Niangara in the Uelle District and in the Ruzizi Valley are indistinguishable from *atactus* of Upper Guinea. Who can say that the whole Upper Guinea race may not have arisen by such crossing between a forest and a savanna form, at one time much more completely segregated?

The interbreeding of the sparrows, *Passer domesticus* and *P. hispaniolensis*, in the Mediterranean region—as Professor Stresemann reminds me—constitutes another example of interspecific hybridism in a restricted area. There, too, the explanation is ecological (Meise, 1936).

I shall close with what is admittedly an analogy, drawn from the human inhabitants of Africa. The Pygmies today are largely restricted to the rain-forest area of Lower Guinea. Yet many anthropologists would agree that this pygmy population was formerly much more widespread. It has retained its peculiarities by taking refuge in great areas of forest where the larger negroes can make their homes only after the heavy labor of clearing land for farms. When annoyed, the Pygmies withdrew farther into the forest, for they found their living by hunting. As a rule a Pygmy man did not take a wife from among the larger negroes because she could scarcely adapt herself to living a nomad life in the forest. The larger negroes did occasionally take Pygmy women to wife, but the offspring were apt to join the population of their agricultural fathers, and the Pygmy characteristics were soon greatly diluted. It was the Pygmies in their forest who remained so distinct. Near some of the borders of the Ituri Forest, in relatively recent times, there must have been considerable Pygmy-Bantu intermarriage. I have seen groups of so-called Walese who showed plainly by their features and their stature that they had a large proportion of Pygmy blood. Whenever Pygmies take up agriculture and settle in relatively permanent villages near the Bantu, this intermingling of genes will certainly take place. And so it must be with the forest-dwelling paradise flycatchers when they find their forest homes dwindling, even though with a larger area of forest available they would continue as what we may still justly call distinct species.

Summary

1. Only three species of paradise flycatchers (*Terpsiphone*) inhabit continental Africa. Two of them, *T. rufocinerea* and *T. rufiventer*, are mainly restricted to heavy lowland rain forests in western and central Africa, both living side by side in the Lower Guinea Forest. The third species, *T. viridis*, is very widely distributed over the African savannas, occasionally invades mountain forests, and occupies clearings and areas of second growth in the Guinean forests.

2. A natural hybrid between the two forest species, *T. rufocinerea* and *T. rufiventer*, is discussed.

3. There is marked polymorphism among males of the more equatorial and northern races of *T. viridis;* but beyond that there is a further variability of *T. rufiventer* and *T. rufocinerea* in certain definite regions, to be explained only as the result of hybridization.

4. Rather extensive populations are found in three distinct areas, always near the outer border of the lowland forest region, which appear to have originated by interbreeding between *T. viridis* and either *T. rufiventer* or *T. rufocinerea*. These areas are in and near Portugese Guinea, Uganda, and northwestern Angola. The characteristics of the hybrid populations in the different areas are just those to be expected, in view of the racial characters of the parent forms.

5. It is suggested that the breakdown of reproductive isolation between *T. viridis* and the two forest-dwelling species is due to fragmentation of the forested areas and the invasion by *T. viridis* of isolated and diminishing patches of forest. This species, under other conditions, shuns the primary rain forest preferred by *T. rufiventer* and *T. rufocinerea*.

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CLIMATE AND EVOLUTION IN WESTERN NORTH AMERICA DURING MIDDLE PLIOCENE TIME

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INTRODUCTION

My studies of late Tertiary floras indicate that those of Middle Pliocene age reflect a semiarid climate, milder and warmer than exists at present in the western United States. This climate was of a highly distinctive type for it finds expression in all known Middle Pliocene floras even though vegetation during this stage was diversified, changing rapidly in composition with latitude and position with repect to the ocean and mountain ranges. Middle Pliocene climate differed sufficiently from that prevailing earlier in the epoch to have greatly modified vegetation over the western United States. As judged from comparative studies of Pliocene floras, there appears to be good evidence for relatively rapid evolution of both species and vegetation during the middle of this epoch. In order to understand more clearly the nature of mid-Pliocene climate, and to discuss its general implications, it is desirable to review first the outstanding features of Middle Pliocene climate as interpreted from fossil floras of this age in California, the Great Basin and border areas, and the High Plains.

With respect to the interpretation of these floras, paleobotanists now consider that most trees and shrubs of late Cenozoic age are essentially identical with the living. Close relationship is indicated not only by details of leaf and seed morphology, but also by the regular association of fossil species in assemblages which are duplicated closely by modern communities. By reference to the present day climate in which similar communities survive, it is possible to infer the former conditions under which equivalent late Tertiary floras lived. In a reconstruction of past climate, analysis is based not so much on the modern occurrence of a particular species as on the assemblages represented in a given flora. This is because individual species, such as the living aspen (*Populus tremuloides*) or sandbar willow (*Salix exigua*), are not always restricted in climatic relations and may therefore be untrustworthy as close indicators of climate. Since each late Tertiary flora commonly includes members of two or more communities whose modern counterparts are confined to climate which may be defined within rather narrow physical limits, each flora can be considered as an indicator of climate. Interpretation on this basis provides insight into the conditions under which vegetation lived during late Tertiary time (Chaney, 1938a).

CLIMATE

Central California

The Middle Pliocene floras of central California, such as the Mulholland (Axelrod, 1944b), Oakdale (Axelrod, 1944c) and Petaluma (Axelrod, 1944d, pp. 186–187), are dominated by live-oak woodland. Associated woodland species, distributed in such genera as *Celtis, Lyonothamnus, Platanus, Populus, Robinia, Salix* and *Sapindus,* now find their nearest relatives in California, the southwestern United States and northern Mexico. Chaparral also has an important place in these floras, the association of species of *Arctostaphylos, Ceanothus, Cercocarpus, Dendromecon, Fremontia, Mahonia, Photinia, Quercus* (scrub-oak) and *Rhus* showing

relationship to living California and Arizona communities. In the Mulholland and Petaluma floras near the coast occur a few records of the forest that lived in bordering upland areas. These include species of *Alnus, Arbutus, Cornus, Fraxinus, Populus* and *Prunus* whose nearest descendants are in the border-redwood forest of central California, as well as species in such genera as *Acer, Berchemia, Nyssa, Populus, Quercus* and *Ulmus,* whose closest equivalents are in the temperate forests of eastern North America and eastern Asia. The dominant live-oak woodland indicates a climate warmer and drier than at the respective fossil localities today. It is inferred that rainfall varied from 15 to 17 inches over the lowlands to 23 inches in nearby forested uplands, and was distributed as summer showers and winter rains. Winters appear to have been more mild than those now found in central California.

These Middle Pliocene floras differ greatly from Lower Pliocene communities in the same area. The Diablo (Axelrod, 1944e, p. 213), Black Hawk Ranch (Axelrod, 1944a) and Two-Mile Bar (U.C. Mus. Pal.) assemblages are characterized by species in such genera as *Betula, Persea, Platanus, Populus, Smilax* and *Ulmus.* Their nearest modern equivalents are in areas of summer rain in eastern North America and eastern Asia. Semiarid, sclerophyllous woodland and chaparral communities such as those just referred to are rare or absent, in contrast to their dominant role in the Middle Pliocene. Minimum rainfall is estimated to have been near 25 to 30 inches over the lowlands in the Lower Pliocene, as compared with 15 to 17 inches for the middle of the epoch. Temperatures were more moderate early in the Pliocene, with lower ranges and extremes. The warm, dry character of Middle Pliocene climate is further emphasized if comparison is made with Upper Pliocene floras such as the Sonoma (Axelrod, 1944d) and Santa Clara (Dorf, 1930) in this region. They show that redwood forest and associated communities were able to extend out over lowland areas because of increased rainfall and lowered temperatures following Middle Pliocene time. Middle Pliocene floras therefore seem to represent vegetation that lived in central California during the hottest and driest stage of the Pliocene.

Southern California

The Middle Pliocene Mount Eden (Axelrod, 1937; MS) and Piru Gorge (Axelrod, MS) floras of southern California were also dominated by woodland, with live-oaks common in both floras and with fossil digger pine also abundant at Mount Eden. Associated woodland species, in such genera as *Cupressus, Juglans, Persea, Platanus, Populus, Salix* and *Sapindus,* find their nearest relatives in southern California, the southwestern United States and northern Mexico. Chaparral is also well represented by *Arctostaphylos, Ceanothus, Cercocarpus, Fraxinus, Fremontia, Quercus, Rhamnus* and *Rhus.* Furthermore, the Mount Eden has such desert-border plants as *Baccharis, Cercidium, Chilopsis, Condalia, Ephedra* and *Prunus* (*Emplectocladus*), and an arid subtropical scrub with *Dodonaea, Eysenhardtia* and *Ficus.* The Piru Gorge flora includes the palm *Sabal* in this latter vegetation. Plants from upland communities are represented in the Mount Eden and Piru Gorge floras, the former including species in such genera as *Amorpha, Arbutus, Philadelphus, Pinus* and *Pseudotsuga,* the latter with *Acer, Populus* and *Salix.* Rainfall in the Mount Eden basin is inferred to have been as low as 12 to 15 inches, increasing to 18 or 20 in the bordering hills, and distributed as summer showers and winter rains. The Piru Gorge flora suggests a total yearly rainfall near 17 inches over the lower basin, increasing to about 20 inches in the nearby uplands. The presence of arid subtropical scrub in both floras, and the occurrence of desert-border species of Sonoran alliance at Mount Eden, suggests

winters were mild, with frosts rare and of short duration.

Current studies of late Miocene and early Pliocene floras in southern California, which include the Puente, Mint Canyon and Repetto, show that woodland was also the dominant vegetation type. But the nearest descendant species have more mesic requirements than those represented in Middle Pliocene floras, with greater numbers being found now in Mexico. These floras also have a larger representation of arid subtropical scrub than those of Middle Pliocene age, and contain species with equivalents in the subtropical short-tree forest of northern Mexico. They accordingly suggest milder climate and higher rainfall than those of Middle Pliocene time, which seemingly was the warmest and driest stage of the epoch in southern California.

Northern Great Basin and border areas

The Middle Pliocene Deschutes flora of central Oregon (Chaney, 1938b) and the Alturas of northeastern California (Axelrod, 1944g) largely resemble vegetation like that found today in open country along streams below the pine-fir (*Pinus ponderosa-Abies concolor*) forest in the nearby mountains. The Deschutes includes *Acer, Populus* (2 spp.), *Prunus* and *Salix*, while the Alturas has *Crataegus, Populus* (3 spp.), *Salix* (3 spp.) and *Ulmus*. The absence of typical forest species in both these Middle Pliocene floras suggests that forest was restricted to moister uplands, away from lowland sites of deposition during this stage. As judged by similar living communities, annual rainfall probably ranged from 15 to 17 inches in the Alturas and Deschutes areas, distributed in the summer and winter months. Milder winters are indicated by the small-leafed ecotype of black cottonwood (*Populus alexanderi*), as discussed below, and by the distribution of certain other living equivalent species in warmer regions to southward.

These floras differ greatly from those of Lower Pliocene age in the nearby area. The Alvord Creek flora, for example, is dominated by forest, with fossil species of *Acer, Abies, Amelanchier, Mahonia, Picea, Pinus, Populus, Pseudotsuga* and *Rosa* most similar to those now in the Sierra-Cascade and Rocky Mountain forests (Axelrod, 1944f). Associates included *Abies, Carpinus, Picea, Prunus* and *Rhus* whose nearest equivalent species are in the temperate, summer-wet forested regions of eastern North America and eastern Asia. The more arid conifer-woodland and chaparral, with species in such genera as *Arbutus, Ceanothus, Cercocarpus, Juniperus* and *Photinia*, apparently occupied exposed slopes near at hand. Minimum rainfall is estimated to have been near 25 inches, or about 10 inches more than that of Middle Pliocene time. The same relationships hold for the lowland regions to northward, as suggested by the Dalles flora from the east end of the Columbia gorge (Chaney, 1944b) and by the Ellensburg flora from south-central Washington (Chaney, 1944d, p. 358). These floras demonstrate the existence of floodplain and adjacent slope-forest communities, with species in such genera as *Acer, Amorpha, Cercis, Liquidambar, Platanus, Populus, Pterocarya, Quercus, Salix* and *Ulmus*. Some of the dominants now have their nearest homologues in the mesic, summer-wet eastern portions of the northern continents. Annual rainfall is estimated to have ranged from 25 to 30 inches, distributed during the summer and winter months.

Central Great Basin

Middle Pliocene vegetation over the present desert region of western Nevada was semiarid woodland as indicated by current studies of the Hazen flora (Axelrod, MS). The Hazen includes only a few species, in *Juglans, Edwinia, Purshia, Rhus* and a live-oak represented by a single specimen. Similar modern communities are found today on the drier borders of conifer- and oak-woodland vegetation in the western United States.

Rainfall is considered to have been near 12 inches yearly, and winters were mild judging from the distribution of similar species in southern California and the southwestern United States.

The Hazen differs greatly from the late Upper Miocene Fallon flora of the same area, which is dominated by live oaks, and also contains *Abies, Castanopsis, Mahonia, Picea, Pinus, Populus* and *Sequoia* (big-tree), plants which survived in this region when minimum rainfall over the lowlands was near 25 inches. The Esmeralda flora of Lower Pliocene age some 100 miles southward is essentially intermediate in composition with respect to the Fallon and Hazen floras (Axelrod, 1940a). Live-oak and conifer-woodland, as represented by species of *Juniperus, Pinus* (fossil digger pine) and *Quercus,* and their associates of *Celtis, Populus* and *Salix,* make up much of the flora. Chaparral includes *Arctostaphylos, Cercocarpus,* and *Rhus,* and desert-border species of *Mahonia* and *Prunus* (*Emplectocladus*) lived on nearby exposed slopes. Forest species of the type represented earlier at Fallon are not known at this later date when rainfall apparently averaged about 18 inches over lowland areas; they may have lived in more mesic sites in the adjacent hills, well-removed from accumulating sediments.

Southern Great Basin

Middle Pliocene floras are unknown from the Mohave Desert. To judge from the temporal succession of vegetation in the northern and central Great Basin, it seems reasonable to assume that the Ricardo flora (Webber, 1933; Axelrod, 1939, pp. 78–83), which is representative of Lower Pliocene vegetation in the Mohave region, had been modified considerably by Middle Pliocene time. The Ricardo flora, as known from fossil woods, includes live-oak and conifer-(pinyon) woodland, with associates of *Cupressus* and *Robinia.* A palm, possibly *Sabal,* suggests arid subtropical scrub vegetation in stream valleys over the region. Leaves collected recently from the Ricardo formation add *Acacia* to the arid subtropical scrub. The presence of *Ceanothus* suggests a nearby chaparral and *Lycium* leads to the inference of a desert-border community in the area. Climate is considered to have been semiarid, with rainfall near 15 inches yearly and distributed as summer showers and winter rains. Temperatures are inferred to have been high in summer, but winters apparently were mild and without prolonged frosts.

The transitional Lower to Middle Pliocene Anaverde flora from the Palmdale area at the edge of the desert 80 miles southwest of Ricardo provides important information as to the nature of floristic modification that may have resulted from Middle Pliocene climate (Axelrod, MS). The Anaverde is dominated by live-oaks, with associates of *Persea, Pinus* (fossil digger pine), *Platanus, Populus* and *Sapindus.* A nearby chaparral is represented by *Ceanothus, Quercus* (scrub-oak) and *Mahonia,* and arid subtropical scrub includes *Colubrina, Dodonaea, Eysenhardtia* and a palm. Annual rainfall is estimated to have been near 15 inches, distributed in the summer and winter months, and winters were mild, with frosts rare or absent. Since minimum rainfall at the edge of the Mohave province was about 15 inches at the end of Lower Pliocene time, it is estimated that precipitation farther out in the desert region probably was near 8 to 10 inches during the Middle Pliocene; this of the same order of change that took place in the region immediately northward. As inferred from the arid subtropical scrub at Anaverde, Middle Pliocene climate over the Mohave region probably was mild and warm at this later date when trees probably were limited to stream-and lake-borders over the lowlands which were now largely covered by desert grassland.

High Plains

Floral succession in the High Plains roughly parallels that in the Great Basin area. The Middle Pliocene Logan County

flora from western Kansas includes only hardy members of floodplain vegetation (Chaney and Elias, 1936). These are in *Celtis, Populus, Ulmus* and a legume, probably *Amorpha*, plants like those that today range westward along stream-valleys into semiarid open plains country in the High Plains. A flora collected recently from near Channing in northwestern Texas includes a small-leafed white oak, *Populus, Sapindus* and other xeric types. Both floras suggest an annual rainfall near 20 inches, distributed in summer and winter, and milder temperatures than those now in the region. These floras differ greatly from the Lower Pliocene Beaver Creek flora of western Oklahoma at the same longitude, where comparatively mesic floodplain vegetation includes species of *Acer, Bumelia, Fraxinus, Gymnocladus, Platanus, Sapindus* and *Ulmus*. Related modern communities now characterize floodplain vegetation some 150 miles eastward where rainfall is 15 inches higher. The Beaver Creek species of *Celtis* and *Ulmus* have larger leaves than those from the Logan County flora. This seems to be a reflection of the more arid climate of Middle Pliocene time (Chaney and Elias, 1936, pp. 23–24).

Discussion

The floras reviewed above provide strong evidence for the presence of mild, warm and dry climate over lowland areas in the western United States south of Lat. 42° during Middle Pliocene time. They differ greatly over this wide area due to the effects of latitude, local relief and position with respect to the ocean and mountain barriers. But all of them, whether we consider the Deschutes of border-forest composition (Chaney, 1938b), the Mulholland of xeric woodland character (Axelrod, 1944b), the Mount Eden of desert-border aspect (Axelrod, 1937) or the Logan County flora of border-floodplain species (Chaney and Elias, 1936), reflect a climate consistent in character from north to south and east to west, the average expression of which was semiarid and warmer than at present. Floras from the Pacific slope suggest a climate as dry as or slightly drier than that at a given locality today. This relationship is obscured in the present desert and steppe regions to the lee of the Sierra Nevada-Cascade and Rocky Mountain axes. Rainfall continued to decrease over those areas as the mountains were elevated and rain-shadows to their lee continued to expand in area during the latest part of geological time. As a result, these interior regions now have a climate which is drier than that which existed at any time in the Tertiary, and they also are colder.

These Pliocene floras express not a uniform climate, but rather the local variations in a semiarid climate which would be expected from differences in latitude, relief and position with respect to mountain barriers and the sea provided the assemblages concerned were contemporaneous. Doubt concerning their general age agreement might be well-founded in the judgment of a tradition-bound stratigrapher, for only one species has been recorded which was common to each region during the Pliocene. This is the Pliocene aspen, *Populus pliotremuloides*, the nearest equivalent of which, *P. tremuloides*, is the most widely distributed tree in North America today. In other words, there are as few woody species common to these fossil floras as are known to be common to the present floras of the High Plains, the Great Basin and California. Nevertheless, two lines of evidence indicate that despite their diversity, these floras were contemporaneous and that all are Middle Pliocene in age.

First is the association with most of these floras of mammalian faunas that are generally considered to be Middle Pliocene (Hemphillian) in age. Second is the evidence which is derived from an understanding of the *clisere*, that is, the temporal succession of vegetation within a given region in response to climatic change. A complete Tertiary clisere, wherein several vegetation types successively replaced one another through this

period of geologic time as a result of changing climate, is unknown for any region. However, sufficient partial series are represented by the known floras of each paleobotanical province so that the age of any given flora can be determined with a high degree of reliability by local correlation. It is possible to show by a more extended analysis than can be entered into here that although these Pliocene communities are diverse, each represents a stage in the floristic evolution of a particular region, and that these stages are contemporaneous (Axelrod, 1944e; 1944g, pp. 278–279). Taking into account the differences in latitude and topography, they form a pattern consistent with the succession of vegetation in each province through Pliocene time. Warm, semiarid climate is so well reflected by the different types of Middle Pliocene vegetation that it provides another means for correlating dissimilar floras over wide areas.

Briefly summarized, the regional aspects of vegetation over lowland areas in the western United States during Middle Pliocene time were as follows:

California: Maximum expansion of woodland and chaparral in central California. A desert-border aspect to these communities in interior southern California.

Great Basin: Largely a riparian distribution for trees over the region now desert. Border-forest at the north and border-woodland at the south. Extensive grasslands over the adjacent plains.

High Plains: Border-floodplain vegetation along stream valleys in open, grassland country.

The warm, mild climate reflected by these Middle Pliocene floras may represent more than a purely local development in the western United States. Vegetation of similar character existed at this time in Europe. If it can be demonstrated that European Pliocene floras reflect a similar climate for the Middle Pliocene and a similar trend through the epoch, then we may have at hand a useful tool for further correlation. With this end in view some of the major review papers of European floras were studied to determine whether they show a similar climatic trend (Depape, 1928; Reid, 1924; Szafer, 1946). Most of the European floras are from higher latitudes than those of the western United States, in areas of moist temperate climate where the Arco-Tertiary Flora was dominant. The majority are north of Lat. 40°, well removed from the effects of dry climate that existed to southward. Furthermore, since ocean-controlled climate extended much more widely over western Europe than the western United States during the Pliocene, dry climate was not so prominent at corresponding latitudes in Europe. The mesic European floras would therefore hardly be expected to show as conspicuously the effects of this climate. What is needed most for comparison is a clisere from northern Africa, a region where the climate may be supposed to have more nearly paralleled that in the western United States.

Available data suggest Middle Pliocene may also represent the warmest stage of the epoch in Europe. Depape (1928) has shown there is a prominent Canary Island Element in the Middle Pliocene of southern France. Members of this group, which now find their nearest relatives in the summer-foggy uplands of the Canary Islands, are known from the Miocene and Lower Pliocene of Europe, but they seem to be more conspicuous in Middle Pliocene (Plasiancian) time and may be valid evidence for warm climate. A semiarid sclerophyllous Mediterranean Element has been recorded with elements of the Arcto-Tertiary Flora at several southern European localities, and it apparently had a more prominent place in the Middle Pliocene (Plasiancian) than earlier (Pontian) or later (Astian) in the epoch. These sclerophylls may represent members of an arid Tertiary Flora at the northern limits of its range in the Middle Pliocene, the stage of its maximum expansion,

thus corresponding generally to the Madro-Tertiary Flora of North America. Warm climate apparently was typical also of the Middle Pliocene of central Europe, as judged by a comparative analysis of several floras (Szafer, 1946). Another indication of changing conditions is the sudden decrease in the relative percentage of the East American and East Asian Elements in Middle Pliocene floras of western Europe as compared with those of Lower Pliocene age (Reid, 1920). These floristic changes clearly reflect important modifications in climate during the middle of the epoch. Although it is hazardous from this distance to regard the data as more than suggestive, it is nonetheless felt that further careful study of the floras available may provide definitive evidence for warm, mild Middle Pliocene climate in Europe. If such a climate is contemporaneous with that in western North America, it may well be part of a world-wide climatic trend which is reflected in Middle Pliocene floras elsewhere. The existence of such a climate would provide a sound basis for wide correlation.

Evolution

Species

Not only the plant assemblages of Middle Pliocene age indicate a semiarid climate warmer than at present, but also certain of their constituent species which have close living counterparts. Some of these fossil plants seem to bear the same relation to their present equivalents that living ecotypes of a given species bear to one another. Fossil ecotypes appear to be represented in several genera, including *Acer, Amelanchier, Platanus, Populus, Quercus, Rosa* and *Ulmus* (Chaney, 1938b, pp. 212–213; 1944a, pp. 12–17; Axelrod, 1941; 1944c, p. 155; 1944f, pp. 241–243; 1944g, pp. 256–262). In each case during the Pliocene the morphology of the leaf is such as to indicate a difference in water-relation as compared with that of the Miocene. The Pliocene species suggest adaptation to drier climate, inasmuch as they resemble most closely populations of the present-day species which exist in the more arid parts of their ranges. A typical case in point is provided by *Populus alexanderi* Dorf, a common Pliocene cottonwood.

P. alexanderi is a fossil homologue of the living *P. trichocarpa* which ranges from Alaska into southern California. The leaves of *P. alexanderi* are uniformily small and approach in size and shape only those produced by *P. trichocarpa* in the arid section of its range in south-central and southern California; the larger leaves found in the more mesic areas of its distribution resemble those of *P. cotremuloides*, a common Miocene species. The contrast between the Pliocene and the present-day species is especially notable in the Deschutes, Alturas and Verdi floras, near which the living equivalent still survives. At the Verdi locality, on the banks of the Truckee River a few miles west of Reno, leaves of *P. alexanderi* can be recovered from rocks which lie within the shade of *P. trichocarpa*. But the leaves of the living species are regularly two and three times the size of the fossil. Leaves which match the fossils in all details of size, shape, margin and texture can be collected only from trees of *P. trichocarpa* which now live some 300 miles southwestward under mild and semiarid climate. The presence of oak woodland and chaparral species with *P. alexanderi* at Verdi, and their occurrence today with the small-leafed ecotype of the modern black cottonwood, corroborate the suggestion of mild, semiarid climate in the Verdi region during Pliocene time.

The appearance and spread over wide areas of fossil ecotypes of arid requirements during the Pliocene suggests strongly that this epoch was marked by major environmental changes of regional extent. The nature of these modifications have been outlined above for the Pliocene in several paleobotanical provinces in the western United States, and more detailed analysis have been presented elsewhere (Axelrod, 1944e; Chaney, 1944c). One

of the major environmental innovations that seems to have resulted from the change to relatively drier and hotter Middle Pliocene climate was that arid grassland and sub-desert vegetation now apparently attained an area *subcontinental* in extent as more mesic vegetation withdrew to moister and cooler sites in bordering areas. Similar communities are known to have been in existence during the Miocene, but they were restricted largely to the borders of forest and woodland which were the dominant types of vegetation over the lowlands of the western United States during this epoch. Species populations which had been developing in these localized open sites may have spread widely and evolved rapidly in Middle Pliocene time, for suitable environments apparently came into existence over wide areas during this stage.

Biologists are now agreed that the principal factors which govern rates of evolution are the organism-environment relation (Clausen, Keck, Hiesey, 1941; Simpson, 1944; Stebbins, 1948). Rapid evolution, it is believed, takes place at times of extensive climatic and topographic changes if there is sufficient genotypic plasticity to provide the materials for diversification. The newly-expanded Middle Pliocene environments appear to have been especially suitable for certain genetically variable groups, particularly of herbaceous and semi-woody habit. Spreading as the dry environments rapidly increased in area, species groups in such families as the Compositae, Leguminosae, Gramineae, Labiatae, Polemoniaceae, Cruciferae, Boraginaceae and others, may have become rich in diverse categories, such as ecotype, ecospecies and coenospecies. Fossil evidence to substantiate this belief is provided by recent studies of Miocene and Pliocene grasses and herbs (Elias, 1942). The data show clearly that in western Kansas and Nebraska species were changing only gradually in Miocene and early Pliocene times. But Middle Pliocene was the stage of greatest diversification of fossil types, with a "literal outburst of these species in Ash Hollow or medial Pliocene time" (Elias, 1942, p. 118, pl. 17). It seems likely that they developed in the new regional environments that came into existence as a result of the warm and mild semiarid climate of Middle Pliocene time. Such an interpretation finds support in recent cytogenetic studies which show that allopolyploids often are more vigorous than the parental forms. Allopolyploids commonly attain geographical distributions which greatly exceed those of their parents. They frequently occupy areas which have been newly opened to colonization, whereas the parental forms are left in the geologically older, relic areas (Stebbins, 1947, pp. 152–155, see refs.). The results of an environmental change of a type affecting an area subcontinental in extent, such as that suggested by these Middle Pliocene floras, would probably be first, a restriction of ancestral species to localized relic environments (or to eliminate them), and second, an expansion over the newly-opened environments of more vigorous, better-adapted forms. In brief, Middle Pliocene seems to have been a time when a great modernization of herbaceous and semi-woody plants of arid grassland and semi-desert environments took place. A noteworthy fact in this connection is that only the Middle Pliocene fossil grasses from the High Plains resemble the modern; the older species seem to have no close modern counterparts (Stebbins, 1947, p. 154).

With the continued diversification of topography due to large-scale mountain building in post-Middle Pliocene time, a host of new and more localized habitats came into existence. These were not only in the newly-elevated mountains, but also over the adjacent lowlands. Furthermore, under the impact of fluctuating Pleistocene climates these environments were in a state of continual flux. In such areas a wealth of new entities may have arisen in latest Cenozoic time, further differentiating from their mid-Pliocene ancestors. Many new forms may thus

have evolved in latest Cenozoic time due to the selective influence of rapidly developing and fluctuating localized environments which became successively more narrowly limited in extent. This apparently accounts for the wide ecological diversification of these herbaceous types which show such a high degree of adaptation in the utilization of geologically recent, highly localized habitats. Differentiation of the various categories has been limited largely by the genetic variability of the populations and by the diversity of localized environments. Nonetheless, the relatively short time that these highly-localized environments have been in existence may well account for the low degree of differentiation of many of the categories, and for the rapid evolution that is continuing today.

Vegetation

Middle Pliocene climate seems to have set the stage for accelerated evolution not only of species but also of vegetation. Changes in the composition and distribution of vegetation during each epoch of the Tertiary were continuous and gradual. These changing floristic and time-space relations are so apparent that they form a sound basis for age determination (Chaney, 1936; Axelrod, 1938; 1944e). Floristic changes during Middle Pliocene and later times appear to have been more rapid than earlier in the Tertiary. The changing and extreme climates to which the major continental Tertiary Floras responded in late Tertiary time largely account for their final breakup and segregation into more narrowly limited regions. These segregates represent the modern descendant units of vegetation. To interpret the evolution of living derivative communities in the Far West, cognizance must be taken of the general trend of climatic change following mid-Pliocene time. This essentially involved the disappearance of effective summer showers and the lowering of winter temperature. A few examples of the general pattern of floristic evolution initiated in the Arcto-Tertiary and Madro-Tertiary Floras by mid-Pliocene and succeeding climates are summarized in the following pages.

Montane forest

Most of the important trees and shrubs now characterizing the Redwood, Sierra-Cascade, Rocky Mountain and North-coast Conifer forests have close equivalents in the West American Element of Miocene floras from the Columbia Plateau and adjacent areas. These species are in such genera as *Abies, Acer, Alnus, Amelanchier, Betula, Castanopsis, Chamaecyparis, Cornus, Fraxinus, Gaultheria, Libocedrus, Lithocarpus, Mahonia, Rhododendron, Rosa, Salix, Sequoia, Sorbus, Thuya, Tsuga* and *Vaccinium*. Regularly associated with them are fossil species that find their nearest relatives in the temperate, summer-wet eastern portions of North America and Asia. In the East American Element are fossil species in such genera as *Carya, Carpinus, Castanea, Fagus, Liquidambar, Nyssa, Taxodium* and *Ulmus*, whose closest counterparts are now found in eastern North America; these genera are no longer indigenous to the region west of the Rocky Mountains. Also included in this element are fossil species of *Acer, Betula, Crataegus, Fraxinus, Populus, Prunus, Smilax, Quercus* and *Vaccinium* which have their nearest relatives in eastern North America. Members of the East Asian Element are distributed in *Ailanthus, Cercidiphyllum, Ginkgo, Keteleeria, Metasequoia* and *Pterocarya*, genera no longer indigenous to North America; in species of *Carya, Hamamelis, Hydrangea, Ostrya, Lindera, Sassafras* and other genera that are represented also in eastern North America; and in certain fossil species of *Acer, Abies, Picea, Populus, Quercus* and *Prunus* which have their nearest homologues in the temperate forests of eastern Asia. The regular association of members of all three elements in fossil floras of Oregon and adjacent areas suggests Miocene forests of generalized composition surviving under a climate of ample rain-

fall distributed rather evenly throughout the year, and moderate ranges and extremes of temperature. Distinct associations are recognizable over the region, with dominant species changing in response to elevation, and position with respect to low mountains or broad coastal valleys.

This forest was modified greatly during the Pliocene as summer rains gradually lessened. Members of the eastern elements show a continued reduction in numbers through the epoch, both from a quantitative as well as a qualitative standpoint, with the reduction accelerated in post-Lower Pliocene time. Lower Pliocene floras from central California northward regularly include species of the eastern elements in a comparatively important role. Such floras as the Black Hawk (Axelrod, 1944a), Diablo (Axelrod, 1944e, pp. 213), Troutdale (Chaney, 1944c), Ellensburg (Chaney, 1944d, p. 358) and Dalles (Chaney, 1944b) are largely unchanged in basic floristic composition as compared with those of Miocene age. By the middle of the epoch, however, members of the eastern elements were rare and they were now subordinate to species of the West American Element, as well as to those of the Madro-Tertiary Flora in transitional areas to southward. The few remaining relics of these elements, some of which have been interpreted as arid ecotypes, disappeared by the end of the epoch. The warm, semiarid climate of Middle Pliocene apparently was an important factor in their reduction in numbers and it also had an important role in the evolution of the surviving West American Element.

The residual West American Element represented in Middle and Upper Pliocene floras was generalized in character. Differentiation into the modern forests that now characterize western North America was continuous through late Cenozoic time. The nature of this late Cenozoic floristic evolution is suggested by the following examples. The close association of members of the Redwood and Sierra-Cascade Components into Upper Pliocene time in the Coast Ranges of central California shows that they have been differentiated in this region only recently (Axelrod, 1944b, pp. 119–122). Descendants of the Sierra-Cascade forest appear to have been segregated to cooler, upland areas, with redwood persisting in the humid, summer-foggy coastal areas. Members of the North-coast Conifer Component also lived with those of the Sierra-Cascade and Redwood Components into Upper Pliocene time in the Coast Ranges (Axelrod, 1944d). The humid, coastal conifers apparently were restricted to the north-coast region as hotter and drier climate developed over areas of their former distribution at the interior. Representatives of the Rocky Mountain Component, including fossil species closely related to *Acer grandidentatum*, *Populus acuminata* and *P. angustifolia*, persisted in California into Middle Pliocene time, but largely disappeared during the Upper Pliocene, seemingly as summer showers were reduced (Axelrod, 1944b, pp. 122–123).

Woodland

Woodland, with dominant live-oaks and such associated conifers as fossil pinyon pine, juniper and digger pine, makes up a prominent part of the Madro-Tertiary Flora which ranged widely over southwestern North America in middle and later Tertiary times. Members of the Sierra Madrean Element have their nearest equivalent species in summer-wet areas extending from the Cape Region of Baja California across the Sierra Madre of eastern and western Mexico and into the southwestern United States. This element includes plants which are no longer represented generically in California, Nevada or Colorado, such as *Bumelia*, *Clethra*, *Eysenhardtia*, *Ilex*, *Pistacia*, *Robinia*, *Sapindus*, *Ungnadia* and *Zanthoxylum*, as well as certain species of *Arbutus*, *Cupressus*, *Forestiera*, *Fraxinus*, *Populus*, *Quercus* and *Rhus* which now have their closest homologues in areas with summer rains and mild winters.

The California Woodland Element, with species in such genera as *Celtis, Juglans, Lyonothamnus, Platanus, Pinus, Populus, Prunus, Quercus* and *Umbellularia*, finds its nearest relatives making up living California woodland associations.

Both elements lived in close association during middle and later Tertiary times in California. The Sierra Madrean Element was prominent into the Lower Pliocene, has a more limited representation by the middle of the epoch, and largely disappeared from this region during the Upper Pliocene, apparently as summer rains lessened. The California Woodland Element was left as a surviving generalized community as members of the Sierra Madrean Element were eliminated. Differentiation of the California Woodland Element is thought to have been largely in response to temperature relations. Species now characteristic of southern California associations have fossil equivalents in central California and they apparently disappeared from that region as temperatures were lowered late in the epoch (Axelrod, 1944b, pp. 117–119). The interior and coastal associations of southern California seem to have differentiated as hot summers, with resultant high evaporation, developed over the interior region as coastal ranges were elevated in latest Cenozoic time (Axelrod, 1944b, pp. 119). Close ancestors of modern insular endemics of the continental shelf islands of southern California and Baja California had a wider range over the continental area during the middle and later Tertiary. They were seemingly restricted to the milder climate of the insular area during late Cenozoic time as a more continental type of climate, with greater ranges and extremes of temperature, developed over the mainland (Axelrod, 1939, pp. 67–71; 1944b, pp. 118–119).

Members of both the California and Sierra Madrean Woodland Elements are known from late Miocene and early Pliocene floras of central Nevada and a few persisted into the middle of the epoch. They apparently disappeared as summer showers were reduced and as mild winter climate gave way to colder conditions later in the Cenozoic. The surviving pinyon-juniper conifer woodland has been interpreted as an impoverished association of Madro-Tertiary derivation that persisted over the area and became adapted to colder climate (Axelrod, 1940b). A similar history is indicated for the central Rocky Mountains, where the modern woodland is largely pinyon-juniper, and where there are records of Sierra Madrean species associated with pinyon and juniper into Pliocene time.

The woodland of the Cape Region of Baja California is high in endemics, and some of these have fossil representatives in the Miocene and Pliocene floras of California (Axelrod, 1939; MS). Their associates included members of both the California and Sierra Madrean Woodland Elements. The persistence of species of Cape woodland alliance into the Middle Pliocene in southern California shows that the modern association has been restricted to its present area only in latest Cenozoic time. This was due presumably to the elimination of summer rains in southern California late in the Pliocene. Differentiation of this woodland is still in progress, for a few typical California plants, as well as oak-woodland species from the Sierra Madre in Sonora and Sinaloa, are in the Cape Region today.

Chaparral

Chaparral, in such genera as *Arctostaphylos, Ceanothus, Cercocarpus, Dendromecon, Fremontia, Garrya, Photinia, Quercus* (scrub-oak) and *Rhus*, has a large representation in the Madro-Tertiary Flora. Close relationship is apparent with the sclerophyllous associations now in California, Arizona and Coahuila. Although chaparral was an important community in southern California by early Miocene time, it apparently reached maximum regional development in California under the semiarid, mild climate of the Middle Pliocene. This is suggested by its

strong representation in floras of this age in central and southern California.

Tertiary chaparral was more generalized in composition than the modern. Certain species now typical of southern California chaparral are known to have close equivalents in Middle Pliocene floras of central California, where they occur with species whose descendants now characterize the chaparral in that area. The lowering of winter temperature over central California later in the epoch probably accounts for the restriction of certain species to southern California (Axelrod, 1944b, pp. 117–119). Close correlatives of modern coastal chaparral species of southern California have been recorded in Middle Pliocene floras at the interior. They apparently were confined to the coastal region as the Santa Monica Mountains, Puente Hills and Santa Ana Mountains were elevated and colder winters and hotter summers developed over interior southern California in latest Pliocene and Pleistocene times. This seems to account for the differentiation of the coastal and interior associations from the more generalized, ancestral Pliocene chaparral.

Desert

The present desert vegetation of the western United States, as typified by the floras of the Great Basin, Mohave and Sonoran Deserts, is now considered to be no older than Middle Pliocene (Axelrod, 1947). This is suggested by the occurrence of forest, woodland, chaparral and arid subtropical scrub vegetation over the region now desert into Lower Pliocene time. By the middle of the epoch trees were restricted largely to stream- and lake-borders over the lowlands which were now characterized by grassland and subdesert communities of wide extent at a time when rainfall was less than 10 inches yearly. Semi-desert shrubs seem to have gradually displaced grassland as rainfall continued to decrease over the developing desert regions.

The Mohave and Sonoran desert regions in California apparently were part of the same paleobotanical province into Middle Pliocene time. This is suggested by the history of arid subtropical scrub vegetation in the Mohave area during Miocene and Pliocene times. Members of this vegetation, as typified by fossil species in such genera as *Acacia, Bursera, Cardiospermum, Dodonaea, Ficus, Karwinskia, Lysiloma, Pithecolobium, Piscidia, Randia, Sabal* and *Thouinia,* were common here in the Miocene. They were reduced in numbers during the early Pliocene and were largely relictual by the middle of the epoch. They appear to have been restricted southward to the warmer Sonoran region as winter temperatures were lowered and as summer rains were eliminated late in the epoch. The disappearance of these plants from the Mohave area, and the persistence there of hardier, microphyllous shrubs, gives to the Mohave Desert a distinctly shrubby aspect as compared with the arboreal character of the Sonoran. The Mohave Desert flora has a number of species in common with the Sonoran Desert, but these are mostly herbaceous and semi-woody plants, not the distinctive arboreal genera of arid subtropical scrub derivation.

The flora of the Mohave Desert shows greater relationship to that of the Great Basin Desert. Many of the plants common to them are typical today of colder regions and have holarctic affinities. Since climate was sufficiently mild for the persistence of arid subtropical scrub in the Mohave region into Middle Pliocene time, it would appear that many of the Great Basin plants may have invaded the Mohave lowlands only in the latest Pliocene and Pleistocene. Supporting evidence lies in the fact that the vegetation of the central and northern Great Basin area has had largely Arcto-Tertiary affinities from Oligocene time down to the present. Plants of Arcto-Tertiary alliance are unknown from the Mohave lowlands, where the vegetation has been of Madro-Tertiary character throughout the middle and later Tertiary. Since the floras of the present areas of the Mohave and Great

Basin Deserts were largely distinct into Middle Pliocene time, it would appear that their present affinities have been established more recently. This was presumably during late Pliocene and Pleistocene times when cold-winter climate developed over the Mohave region as the province was elevated and mountains were rapidly built up along its western border. The present flora of the Mohave Desert thus appears to be an ecotone. It contains older, hardy species of Madro-Tertiary derivation that became adapted to cold-winter climate, and plants of Arcto-Tertiary alliance that seem to have invaded the area only recently as cold-climate developed over the province.

Discussion

The histories of montane forest, woodland, chaparral and desert vegetation outlined above indicate that the major Tertiary floras of the western United States were differentiated into communities of essentially modern aspect largely by Middle Pliocene and succeeding climates. Differentiation apparently was in response to a trend toward lowered yearly rainfall, shifting seasonal distribution of rain, and increased ranges and extremes of temperature. Under the impact of these accelerated post-Lower Pliocene climatic changes the Arcto-Tertiary and Madro-Tertiary floras lost their identity, since species formerly shared with other regions became extinct in certain areas of their early Pliocene distribution. As montane forest, woodland, chaparral and arid subtropical scrub were restricted in range as rainfall lessened, open steppe and subdesert environments of subcontinental extent came into existence over the warm-dry and cold-dry regions. Herbaceous and semi-woody plants which had a restricted distribution on the borders of Miocene and early Pliocene communities apparently spread widely and evolved rapidly as these new regional environments were initiated. Only in latest Cenozoic time, in response to the development of more localized environments, were the modern plant formations fully segregated into the regional climaxes, the subregional associations and the more localized communities that now characterize western North America.

The floristic evolution initiated during the Middle Pliocene has not been completed, but is continuing at the present time. This is shown by inter-relationships displayed by the various modern communities of each plant formation over this region. The relationships between these living derivative communities of late Tertiary vegetation are expressed by the modern patterns of plant distribution. They occur not only in North America, but extend beyond to other continents in both latitudinal and meridional directions. These distribution patterns are considered to reflect the former occurrence of ancestral Tertiary floras across the intervening areas. The modern patterns seem to have resulted from world-wide late Cenozoic climatic changes which differentiated generalized Tertiary floras into communities now having more restricted ranges. Three important patterns which seem to find an explanation in late Tertiary events are latitudinal, radial and meridional.

Latitudinal pattern is exemplified by the present occurrence of similar communities in such widely separated areas as eastern North America and eastern Asia, western North America and eastern Asia, or western Europe and North America. They are similar not only in having a large number of common genera, but also essentially similar species. Close relationship of many of these species that are scarcely differentiated morphologically is shown by the fact that some of the plants now on different continents are still capable of producing fertile hybrids, even though their populations have been isolated since the Miocene (Stebbins, 1945, p. 85; 1947, p. 152). These latitudinal relationships can be accounted for only on the grounds of segregation of more widely spread and more generalized Tertiary vegetation, with subsequent extinc-

tion in the intervening areas. The fossil record shows that this has been the case, for these patterns find an explanation in the history and development of the Arcto-Tertiary Flora. Examples are provided by the elimination of members of the East American and East Asian Elements from the western United States during the later Pliocene. The extinction of members of the West American, East American and East Asian Elements in western Europe during the Middle and Upper Pliocene also is well-established, and representatives of the West American and East American Elements disappeared from eastern Asia at the same time. The occurrence of identical and closely-related species common to two or more of these regions clearly attests to the former continuity of the Arcto-Tertiary Flora across Holarctica, and the fossil record shows clearly that this has been the case (Chaney, 1940, figs. 1, 2). Subsidiary latitudinal patterns within limited regions, as shown by the relationships between the Redwood, North-coast Conifer, Sierra-Cascade and Rocky Mountain forests in western North America are expressions of continuing segregation through latest Cenozoic time into still more localized environments, as discussed above.

Radial pattern, as illustrated by species in the present arid regions of southwestern North America, finds an explanation in the history and development of the Madro-Tertiary Flora which spread radially over southwestern North America as dry climate expanded in middle and later Tertiary times. The former continuity of the Madro-Tertiary communities recorded in the fossil record, such as oak-woodland, conifer-woodland, chaparral, sage and arid subtropical scrub, has been disrupted to the degree that the more arid, derivative desert vegetation of latest Cenozoic age now separates them. The modern distribution pattern shown by species in the arid communities across southwestern North America reflects late Cenozoic history of the Madro-Tertiary Flora. This largely involved the elimination of species formerly shared with other areas as localized climates developed over the region. Examples of this climatic segregation include the disappearance of fossil equivalents of modern Cape woodland endemics from southern California; the elimination of fossil equivalents of central California woodland species from central Nevada; the disappearance of fossil representatives of central California conifer-woodland species from southern California; the occurrence in northern Texas, central Colorado, central Nevada, southern California and central California of fossil species whose nearest relatives are now in southern Arizona and adjacent New Mexico; and the presence in California of fossil equivalents of species of modern northeast Mexican distribution. If these examples are considered individually one might assume that they represent no more than latitudinal (east-west) and meridional (north-south) patterns. However, when they are all considered together they are clearly radial to one another, and to their general center of origin which was over southwestern North America.

Radial pattern apparently exists elsewhere in the world, though the details are not now known. Arid sclerophyllous vegetation recorded in the middle and later Tertiary floras of southern Turkestan, the Mediterranean basin, southern Africa and South America, may well represent counterparts of the Madro-Tertiary Flora of southwestern North America, a major continental flora of low-middle latitude origin that developed under aridity during the Tertiary and spread radially with expanding dry climate. On this basis, the modern occurrence of arid Mediterranean plants in the mountains east of Lake Tchad, a region now separated from the Mediterranean basin by the North African desert region, might be attributed to a mid-Tertiary sclerophyllous flora that may have extended over the area now desert.

Meridional pattern is exemplified by numerous species in the desert, sage, grassland and arid subtropical scrub vege-

tation in western North America. Many of the plants now making up these vegetation types, which first appear in the Madro-Tertiary Flora, are represented by closely-related species in similar communities in South America. This discontinuous pattern in distribution, which is now interrupted by a wide tropical belt, has been accounted for by north-south migration along arid coastal strips and by lee-slope migration along Tertiary archipelagos extending across the tropics. The weakness of the first interpretation is that arid coasts have a greater extent today than at any time in the past. Since migration of these arid plants is not now effective along this route it seems unlikely that it could have operated during the Tertiary or Cretaceous, for throughout those periods moist, tropical climate was more widespread over lower latitudes than it is today. As for trans-tropic migration on lee slopes of Tertiary archipelagos, there is no clear evidence for the existence of north-south island chains. Trans-tropic migration along any land route seems unlikely for plants of arid requirements during the Tertiary because the intervening region was largely a lowland into late Cenozoic time, and of wet-tropical character. Commencing largely in the later Pliocene and continuing through Pleistocene time, mountain building elevated the central cordilleran region many thousands of feet, and this was followed by the building up of high volcanoes along the mountain chain. Although this orogeny provided a means for north-south dispersal of mammals, it apparently did not affect materially the relationships between the floras of the dry regions north and south of the tropics.

The meridional pattern shown by the dry-climate plants now on both sides of the tropics which have no (or few) intervening stations, may be explained on the basis of the differentiation of wider-ranging Tertiary prototypes in response to similar environments developing over the northern and southern parts of their areas during middle and later Tertiary times. Andrews (1913; 1914) and Bews (1927) have demonstrated clearly the significance of gradually developing dry climate to the evolution of tropical floras. More recently, DuRietz (1940) has suggested that if a trans-tropic polymorphic group differentiated into closely similar forms at the north and south, trans-tropic migration would not be necessary to explain certain distributional problems which involve the occurrence of closely-related species on both sides of the tropics.* With these concepts in mind, and recalling that the Neotropical-Tertiary Flora extended across many degrees of latitude in the northern and southern hemispheres in early Tertiary time (Chaney, 1947), we have a clue to the probable evolution of similar modern vegetation as well as closely-related living species north and south of the tropics.

With the gradual equatorward restriction of tropical vegetation as subhumid climate expanded over low-middle latitudes following the early Eocene, many initially tropical types of wide range may have become adapted gradually to new, border-tropical environments of varying character. Such plant formations as arid subtropical forest, subtropical savanna, arid subtropical scrub, grass, sage and warm-desert appear to have evolved successively on the northern and southern borders of the tropics as aridity increased over lower latitudes during the Tertiary. Available evidence suggests that arid subtropical forest and subtropical savanna were in existence by the end of Eocene time; arid subtropical scrub by the end of the Oligocene; and that grass, sage and sub-desert communities had a localized occurrence in the Miocene, and a

* The writer does not accept DuRietz's application of this hypothesis to his particular problem, which deals with a Cretaceous differentiation of primitive populations along trans-tropical highlands bridges to account for the occurrence of closely-related species in the cold-temperate climates north and south of the tropics. His general concept, however, seems to be a fundamental contribution to problems of plant distribution.

wide regional distribution in the Pliocene. From this standpoint, it is understandable that there are today many species-complexes that extend north-south from the wet tropics and into these derivative, arid tropical vegetations; that there are many species common to several of these plant formations; and that there are closely-related species in the desert, grass, sage and arid subtropical scrub vegetations north and south of the tropics which no longer have intervening tropical stations.

Paired-species in such genera as *Acacia, Caesalpinia, Condalia,* and *Prosopis* which now occur in dry regions north and south of the tropics seem to have evolved through the adaptation of wider-ranging, tropical derivative prototypes to essentially similar environments developing on the northern and southern borders of the tropics by middle Tertiary time. This is suggested by the occurrence of arid subtropical scrub species of essentially modern character in the early Miocene of southern California. A number of them, in such genera as *Acacia, Bursera, Caesalpinia, Colubrina, Dodonaea, Cardiospermum* and *Prosopis,* have close counterparts in living species in Mexico and in South America. Species of arid subtropical alliance are known also from the Oligocene Florissant and Eocene Green River floras, but they are not as nearly related to the living species as those of Miocene age. This suggestion that some of the north-south relations of arid plants now on both sides of the tropics were already established by Miocene time finds support in a current paper by Epling (1948), where he reaches a similar conclusion as based on the relations of the tribe Lepechineae (Labiatae). In connection with the present interpretation of these north-south relations, it should be added that certain insects of Neotropical origin also show a discontinuous distribution between the arid portions of North and South America (Linsley, 1939); they may have had a similar sort of history.

A number of the closely-related, semiwoody and herbaceous plants in the grassland and desert areas at the north and south may have evolved in similar manner, but later in the Tertiary and probably during the Pliocene. It was only during this epoch that populations of grassland, sage and sub-desert communities could exploit fully their genotypic potentialities. Earlier in the Tertiary these communities were relatively restricted in distribution, with ancestral species confined largely to the more localized environments on the sub-humid borders of the tropics where they probably were evolving slowly. The grassy and sub-desert communities appear to have been of generalized composition in late Tertiary time. This is suggested not only by the history of the different kinds of arid vegetation in southwestern North America, as outlined above, but also by certain patterns of trans-tropic distribution. There are species in several areas in southwestern North America that find their austral counterparts in similar restricted regions; these include species common to California and Chile; to the Texas-Chihuahua region and northern and central Argentina; and to the Great Basin and the Argentine Andes and northern Patagonia (Johnston, 1940). Such patterns seem explainable only on the basis of the segregation of more generalized Pliocene communities into similar local climates which developed north and south of the tropics in latest Cenozoic time. These meridional relationships were greater during the Pliocene than they are today, for fossil grasses from the High Plains find their nearest modern relatives in South America (Stebbins, 1947, pp. 153–154); they disappeared from North America in late Pliocene and Pleistocene times.

Summary

Fossil floras from California, the Great Basin and the High Plains suggest a mild and warm semiarid climate characterized the western United States during Middle Pliocene time. This climate seems sufficiently distinctive to provide a basis for inter-provincial correlation of dis-similar

types of vegetation. Warm climate also seems indicated for the mid-Pliocene of Europe and may form a means for wide correlation if substantiated by further investigation.

Middle Pliocene climate is inferred to have had an important role in evolution for it apparently initiated grassland and sub-desert environments of subcontinental extent. Genetically variable populations of herbaceous and semi-woody plants probably spread into these areas from more restricted semiarid habitats already existing on the borders of forest, woodland and scrub vegetation where they had been evolving slowly during earlier parts of the Tertiary. Evolution in the newly-expanded Middle Pliocene environments seems to have been rapid. The continued development of more localized environments over the subcontinental dry regions during post-Middle Pliocene time presumably had a selective role in differentiating various taxonomic categories.

Middle Pliocene and succeeding climates are considered to have been a major factor in the final breakup and segregation of major continental Tertiary Floras into restricted areas, and in their evolution into modern plant communities. Certain fundamental patterns in present-day plant distribution, termed latitudinal, radial and meridional, seem explainable on the basis of this late Cenozoic floristic evolution.

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EVOLUTION OF THE HORNED DINOSAURS

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INTRODUCTION

The horned dinosaurs or ceratopsians are of particular interest to the student of evolution for various reasons. In the first place these dinosaurs are restricted geologically. They were the last of the dinosaurs, appearing at a late stage in the Mesozoic Era and going through the entire range of their phylogenetic history in a relatively short space of geologic time. It is therefore obvious that evolution in the horned dinosaurs was comparatively rapid. Secondly, these dinosaurs are restricted geographically. Except for the ancestral forms which occur in Mongolia, the horned dinosaurs are, practically speaking, limited to the continent of North America. Therefore at the present time the horned dinosaurs may be considered as a group of north Asiatic origin and of North American development. In the third place, the horned dinosaurs show a consistent and rather limited pattern of morphological evolution, as might be expected in a group of such restricted geologic limits and geographic distribution. In the light of these facts, how is the evolution of the horned dinosaurs to be interpreted? What conclusions can be drawn from the evidence of the fossils and of their occurrence?

Before becoming involved in a detailed consideration and discussion of the problem before us it may be useful to review briefly at this place the classification of the ceratopsians, and in addition our knowledge of their geographic distribution and geologic occurrences.

Classification

The Ceratopsia constitute a suborder of the order Ornithischia. Other suborders of this order of dinosaurs are the Ornithopoda, or duckbilled dinosaurs, the Stegosauria, or plated dinosaurs, and the Ankylosauria, or armored dinosaurs. All of the dinosaurs contained within the four suborders of the order Ornithischia are herbivorous types, and rather specialized in their morphology.

The suborder Ceratopsia can be divided into two families, the Protoceratopsidae, or the primitive horned dinosaurs, and the Ceratopsidae, the large, specialized horned dinosaurs. The genera contained within the two families of ceratopsian dinosaurs are as follows.

Protoceratopsidae
Protoceratops, Leptoceratops
Ceratopsidae
Anchiceratops, Arrhinoceratops, Brachyceratops, Chasmosaurus, Ceratops, Eoceratops, Monoclonius, ?Notoceratops, Pentaceratops, Styracosaurus, Torosaurus, Triceratops

Of the above-listed genera, *Brachyceratops* possibly is synonymous with *Monoclonius*, the type species being based upon an immature individual that may be a growth stage of this last-named genus. (Whether or not *Brachyceratops* is a distinct genus, the fact that it is now known only from immature material makes it rather unsuitable for the present study, which is concerned with a comparison of adult animals.) *Ceratops, Eoceratops* and *Notoceratops* are known from such insufficient materials as perforce to be excluded from a discussion of ceratopsian evolution. Therefore, for these reasons the genera *Brachyceratops, Ceratops, Eoceratops* and *Notoceratops* will not be in-

ZOOLOGY

cluded in the present treatment of the Ceratopsia.

Geographic distribution

As mentioned above, the ceratopsians are essentially a group of North American development. *Protoceratops*, the structural ancestral type for the Ceratopsia, is known from abundant materials found in Mongolia. *Pentaceratops* has also been recorded from Mongolia, but upon the basis of a single small element from the frill of the skull—the epoccipital. The genus *Notoceratops*, described by von Huene from South America, is, as already mentioned, founded upon such insufficient materials as to be of little value.

The remaining genera of ceratopsians, including the well defined type species of *Pentaceratops*, are found in the western portion of North America, in Cretaceous sediments of the Rocky Mountain region. Thus, these fossil reptiles are found in a long north and south belt, extending from northern Coahuila and southern Texas and New Mexico on the south well into Alberta on the north.

Geologic range

The ceratopsian dinosaurs are confined to the upper part of the Cretaceous period, even in their most primitive manifestations. In Mongolia, *Protoceratops* occurs in the Djadochta formation, a Cretaceous horizon that upon the basis of present knowledge is difficult to correlate with possible equivalents in North America and Europe. It is probable, however, that the Djadochta is no later in age than the Belly River formation of North America, and it is possibly slightly older than the Belly River.

In North America the Ceratopsia are distributed in three successive stratigraphic horizons of Upper Cretaceous age. The lowest of these levels comprises sediments of the Belly River series in Alberta, and the Two Medicine and Judith River formations in Montana. In the middle level are the Edmonton formation of Alberta and the Kirtland and Fruitland formations of New Mexico. Finally, the upper level, the last phase of Cretaceous sedimentation in North America, consists of the Lance and Hell Creek formations of Montana and Wyoming, the Denver and Arapahoe beds of Colorado and the Ojo Alamo and McDermott formations of New Mexico.

The relationships of these ceratopsian-bearing formations can be indicated as shown on the following correlation chart.

	Mongolia	Alberta	Montana	Wyoming	Colorado	New Mexico
Upper Cretaceous			Lance	Lance Hell Creek	Denver Arapahoe	Ojo Alamo McDermott
		Edmonton				Kirtland Fruitland
		Belly River	Two Medicine Judith River			
	Djadochta					

Adaptive Radiation in the Horned Dinosaurs

It was said in the introduction to this paper that the ceratopsian dinosaurs show a consistent and limited pattern of morphological evolution during their geologic history, and this fact must be kept in mind in a review of the group. It is probably correct to say that in the post-cranial evolution the ceratopsians are on the whole fairly conservative; the skeletons of the last and largest of the horned dinosaurs are essentially large editions of the skele-

ton of *Protoceratops,* the ancestral type, with of course the consequent changes in proportions that take place as a result of growth in size, changes made necessary because of weight problems. It is in the skull that adaptive radiation in the Ceratopsia becomes most apparent, and even here it is not a phylogeny involving great and profound changes. Rather, the pattern of evolution in the ceratopsian skull is a consistent one; or to use a musical comparison, it is composed of variations on a theme.

Before going into the problem of adaptive radiation in the Ceratopsia as demonstrated by the skull it may be well to review briefly the evolutionary trends in the skeleton as a whole. The structural design for the ceratopsian dinosaurs, established in the genus *Protoceratops,* is that of a quadrupedal ornithischian, with an extremely large skull, of which the posterior dorsal bones are extended to form a frill over the neck and shoulder region. In following this structural type from *Protoceratops* to the ceratopsians of Lance times there is a considerable increase in size, an evolutionary trend that is general among all of the dinosaurs, and various developments in skull morphology, developments that will be discussed in some detail below. Moreover, there are certain changes in proportions in the post-cranial skeleton; for instance in the evolution of the ceratopsians there is a definite proportional shortening of the tail and of the limbs. Nevertheless, the basic design holds from the beginning of this evolutionary line to the end, and the changes that take place affect the details of the design without changing its fundamental characters.

The points mentioned above are illustrated by figure 1, based upon measurements of skeletons in the genera *Protoceratops, Monoclonius* and *Triceratops.* It can be seen from this figure that the skull in the ceratopsians was large from the beginning—indeed, it is interesting to note how the proportional size of the skull held to an approximate constant during the adaptive radiation of these dinosaurs. The proportional shortening of the tail and of the limbs are trends that would be expected to accompany increase in size; they are part of a picture of correlated changes in body proportions from light animals capable of fairly rapid movements, to heavy, ponderous beasts. It is known that the ancestral dinosaurs were

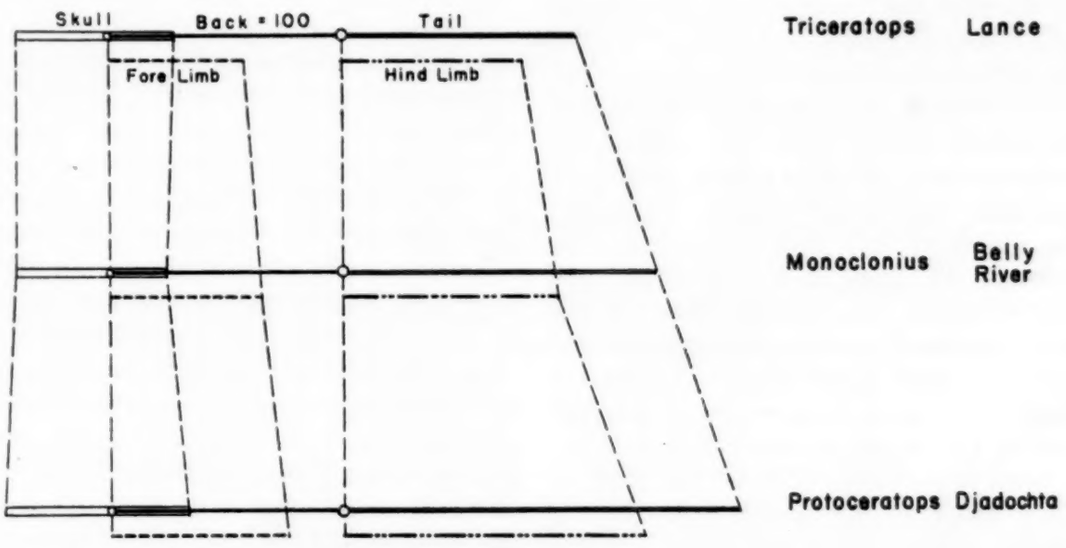


FIG. 1. Skeletal proportions in three genera of Ceratopsia. The length of the back, from the occipital condyle of the skull to the acetabulum of the pelvis, is taken as the unit basis for comparison.

thoroughly bipedal, and that there was a secondary reversion to quadrupedalism in most of the forms that showed definite size increases. Such an evolutionary trend was inevitable as an adaptation to the need for more powerful support in the front quarters for an ever-increasing body weight. Figure 1 shows that this trend to quadrupedalism in the ceratopsians was brought about, not by a relative increase in the size of the forelimbs, as has often been stated, but rather by a relatively great decrease in the size of the hindlimbs. As can be seen from this figure, both fore and hindlimbs suffered a reduction in relative size in the evolutionary sequence from *Protoceratops* to *Triceratops,* but whereas the relative decrease of the forelimbs was slight, that of the hindlimbs was very marked. The net effect, of course, was that of enlargement of the forelimbs as compared with the hindlimbs.

Such were the general trends in the postcranial evolution of the ceratopsians. Let us turn now to a consideration of the evolution of the skull.

In *Protoceratops* the skull is thoroughly ceratopsian. It is extremely large in comparison with the skeleton as a whole. It is deep, and anteriorly the front of the skull and of the lower jaws is compressed into a sort of parrot-like beak. In all of the ceratopsians except *Protoceratops* and *Leptoceratops* this beak is thoroughly edentulous and bird-like, but in these two comparatively primitive genera small premaxillary teeth are retained. Moreover, the maxillary and dentary teeth on the sides of the jaws in *Protoceratops* and *Leptoceratops* are simpler than in the more advanced genera. But these are details of no great significance in this present study. Of more importance is the fact that in *Protoceratops* there is a well developed fenestrated frill on the back of skull, which in life served primarily for the insertion of powerful neck muscles, and secondarily as protection for the cervical region. In the fully adult *Protoceratops* this frill is proportionately almost as large as it is in some of the later ceratopsians. The ontogeny of the frill is known in *Protoceratops,* and this shows that the frill underwent a great proportional increase during development from the newly hatched individual to the mature adult. Finally, there are no horns on the skull in *Protoceratops,* a distinct contrast to the condition in all other ceratopsians.

In tracing the adaptive radiation of the ceratopsian skull beyond *Protoceratops,* we can follow several evolutionary trends developing simultaneously. These are:

1. Reduction and final supression of the premaxillary teeth.
2. Changes in the proportion of the frill.
3. Changes in the fenestration of the frill.
4. Development of nodes and spikes on the edges of the frill.
5. Development of the nasal horn.
6. Development of the supraorbital horns.

From *Protoceratops,* taken as the central ancestral type, the ceratopsians would seem to show a dichotomy so far as the evolution of the skull is concerned, and this dichotomy of the ceratopsians had taken place by Belly River times. On the one hand, there was an evolutionary line characterized by a rather short frill, a line typified by the genera *Brachyceratops, Monoclonius, Styracosaurus* and *Triceratops.* The other line of evolution was that in which the frill became relatively long, and this line is typified by the genera *Chasmosaurus, Anchiceratops, Arrhinoceratops, Pentaceratops* and *Torosaurus.*

The differences in proportional frill length in these two evolutionary lines are not great, but they are none the less well defined when analyzed. In the first group, those genera with the short frill, the frill, or more properly that portion of the skull behind the orbit, has a length less than or at the most, equal to the length of the skull in front of the orbit. In the long-frilled line, on the other hand, the

postorbital length of the skull is considerably greater than the preorbital length.

In both short-frilled and long-frilled lines the frills are fenestrated, except in the genus *Triceratops,* which has a solid frill. There is every reason to think, however, that the solid frill of *Triceratops* evolved from a fenestrated frill. Lull has suggested that the fenestrae in the two lines of ceratopsians were independently derived. In the short-frilled phylum the fenestrae, according to Lull, probably were formed by a perforation of the parietal bones, because in the genera belonging to this group the fenestrae are contained entirely within the parietals, a condition established in *Protoceratops* and continuing to *Triceratops,* in which form the fenestrae are secondarily closed. In the long-frilled phylum, according to Lull's suggestion, the fenestrae were formed by the manner in which the parietal bone grew back and laterally to join the squamosal. "Ancestrally, therefore, the outer limit of the fenestra must have been the squamosal. At the anterior end of the fenestra, behind the supratemporal openings, a plate of bone extends laterally to join the squamosal near its anterior end, and from these transverse portions of the parietal, branches developed forward and backward, as the case may be, extending along the squamosal until they met in an overlapping suture which, at any rate in *Chasmosaurus,* failed to fuse and in one case failed to meet. This now excludes the fenestra from contact with the squamosal and the aperture thus formed is persistent throughout the recorded history of the phylum." (Lull, 1933, p. 24.) Whether or not one accepts Lull's idea of an independent origin for the parietal fenestrae in the two lines of ceratopsians, there is no doubting the fact that these fenestrae were persistent through ceratopsian history.

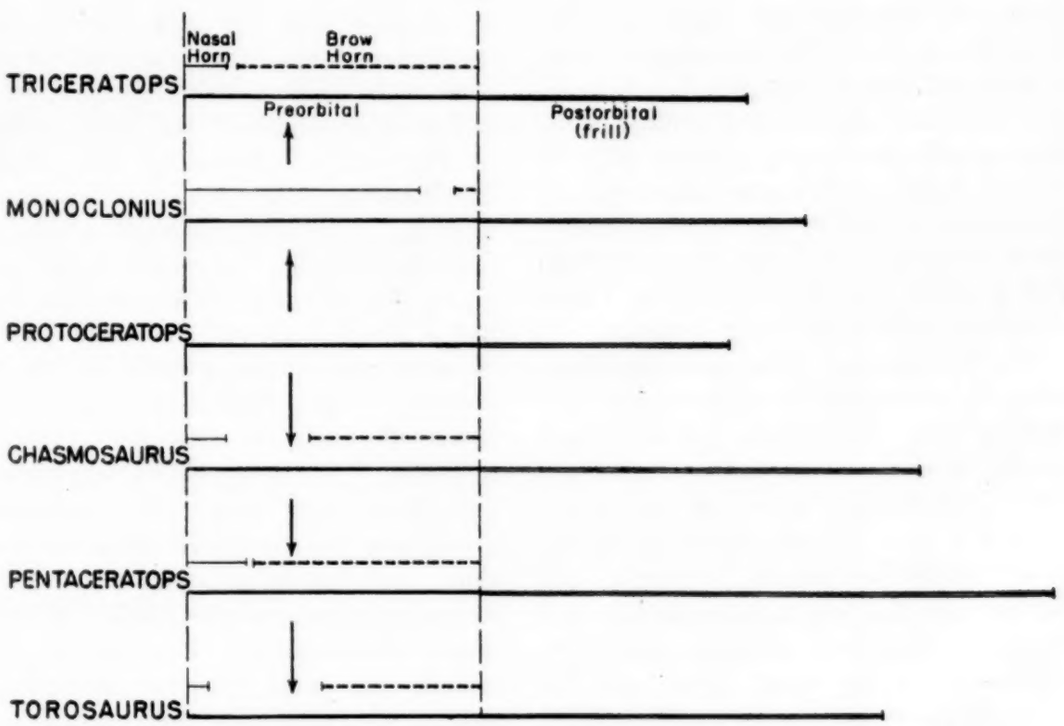


FIG. 2. Proportions of certain parts and elements of the skull in various genera of Ceratopsia. The short frilled genera, *Monoclonius* and *Triceratops,* and the long-frilled genera, *Chasmosaurus, Pentaceratops* and *Torosaurus,* are arranged in geologic sequence as they diverge from the earliest and most primitive genus, *Protoceratops.* The preorbital length is taken as the unit basis for comparison.

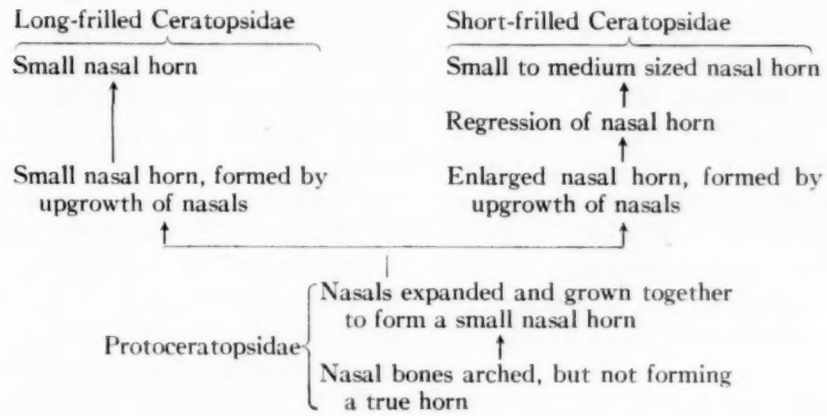
Except for *Protoceratops,* the ceratopsian dinosaurs are characterized particularly by the development of horns and spikes on the skull. There is always a nasal horn and it may be large or small. Generally there is a pair of supraorbital horns, one above each eye, although in some genera these may be so small as to be almost nonexistent. Occasionally there are spikes or nodes around the edges of the frill.

To consider first the spikes and nodes on the frill, these are plainly separate dermal ossifications that during individual growth became fused to the edge of the frill. As such they have been given a distinctive osteological name and are called the epoccipital bones. They appear early in ceratopsian evolution, being characteristic of the Belly River genera *Chasmosaurus, Monoclonius* and *Styracosaurus;* indeed, in this last genus they reach the culmination of their development and form long spikes, radiating laterally and posteriorly from the frill. Subsequent to Belly River times the epoccipitals seem to have suffered on the whole a retrogressive trend in evolution, and in most of the later genera they became much reduced or even disappeared, during which process the edge of the frill either remained crenulated, or in the later forms became smooth and straight. In *Triceratops* of Lance times, the epoccipitals were retained.

The development of the nasal and brow horns is more difficult to interpret than that of the epoccipitals. Brown and Schlaikjer have shown that in *Protoceratops,* even though there are no horns, there is a very distinct uparching of the nasals in old individuals, a morphologic development that might subsequently lead to the formation of a nasal horn. In *Leptoceratops* the nasals grow and become conjoined to form a well-developed horn core, and this process is continued in the genus *Brachyceratops.* Both of these genera show that the horn core is formed by the upgrowth and union of the nasal bones into a single, solid structure. Moreover, in *Brachyceratops* there is on each side a terminal ossicle at the end of the nasal horn, indicative of a dermal element with a separate center of ossification.

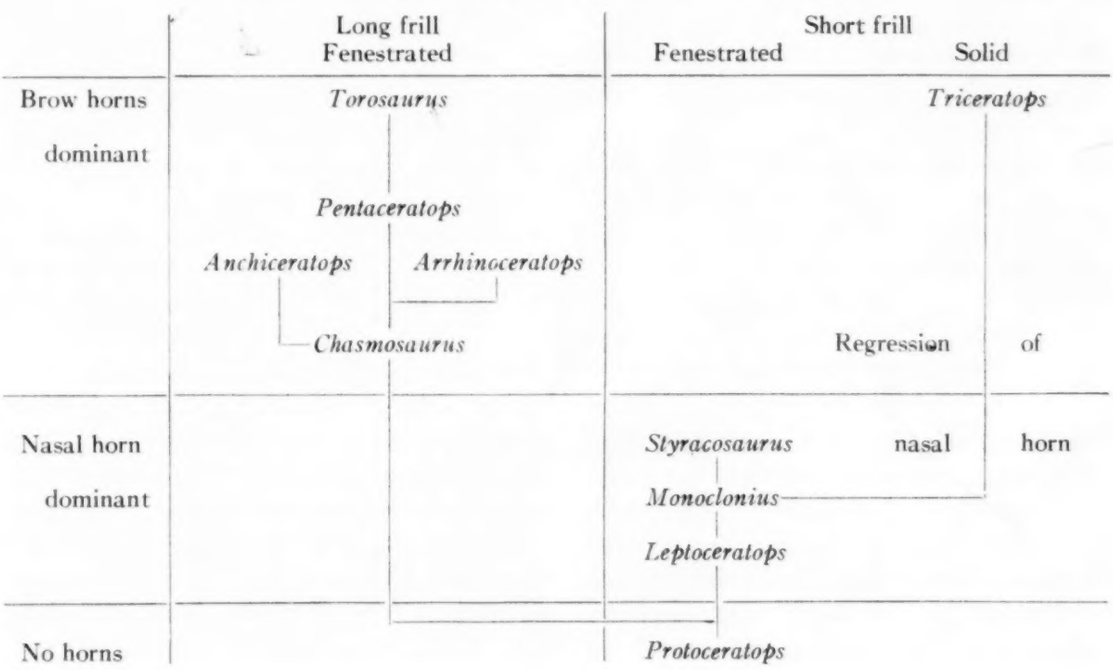
In *Monoclonius* and *Styracosaurus,* characterized by large nasal horns, these horns seem to be formed by an upgrowth of the nasal bones, as in *Brachyceratops,* and the same would appear to be true of the small nasal horns in the various "long-frilled" genera of Ceratopsia. In *Triceratops* the nasal horn is small or of medium size. Brown and Schlaikjer have maintained that the nasal horn is suturally distinct from the nasal bones, and this has led them to think that in this genus there was a regression of the expanded nasal bones and the development of a new nasal horn from dermal ossicles, similar to those seen in *Brachyceratops.* According to this interpretation, then, the nasal horn of *Triceratops* is not strictly homologous with the small nasal horn of the various long-frilled genera of ceratopsians. As against this, however, is recent evidence obtained from some material of *Triceratops* collected by Mr. Charles M. Sternberg of the National Museum of Canada. The new material, which fortunately includes the nasal horn of a young *Triceratops,* shows that the horn in this genus is formed, just as in the case of other ceratopsian genera, by an upgrowth of the conjoined nasal bones. Upon the basis of this new evidence, therefore, it is reasonable to suppose that the nasal horn can be homologized throughout the known genera of ceratopsians, and that in all cases it is formed by an upgrowth of the conjoined nasal bones. Consequently, it is necessary to assume that in the sequence from *Monoclonius* to *Triceratops* there was a considerable regression in size of the nasal horn.

The evolution of the nasal horn in these dinosaurs can be outlined as follows.


Long-frilled Ceratopsidae
Small nasal horn
Small nasal horn, formed by upgrowth of nasals
Short-frilled Ceratopsidae
Small to medium sized nasal horn
Regression of nasal horn
Enlarged nasal horn, formed by upgrowth of nasals
Protoceratopsidae
Nasals expanded and grown together to form a small nasal horn
Nasal bones arched, but not forming a true horn

The brow horns, according to Brown and Schlaikjer, are in each case formed by an upgrowth of the postorbital bone above the eye. In *Leptoceratops* and *Brachyceratops* the brow horns are quite small, and they remain small in the Belly River genera having very large nasal horns, namely *Monoclonius* and *Styracosaurus*. In the other genera of ceratopsians, however, the brow horns show a progressive increase in size, while there is a regression of the nasal horn, as in *Triceratops*, or a lack of growth in the nasal horn, as in the long-frilled ceratopsian genera. In this connection it is interesting to see that among the earlier long-frilled forms, such as *Chasmosaurus*, with rather small brown horns, the nasal horn is moderately large, whereas, in the late genera such as *Torosaurus*, with very large brow horns, the nasal horn is relatively very small. A suggestive parallel to this is to be seen within the genus *Triceratops*. Those species having the smallest brow horns have the largest nasal horn, while those forms having the largest brow horns have the smallest nasal horns. It would appear that there was a correlation in horn development throughout ceratopsian evolution, whereby an increase in the

TABLE 1. *Diagram of horn and frill evolution in ceratopsians*

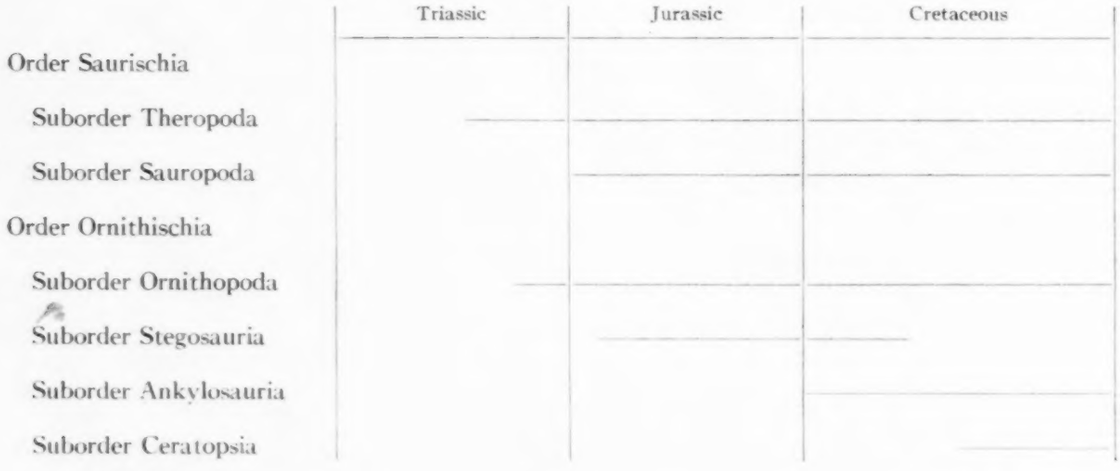


nasal horn retarded development of the brow horns, while an increase in the brow horns retarded the nasal horn.

From the foregoing discussion we see that the ceratopsian skull followed two simultaneous lines of adaption during upper Cretaceous times and within each of these lines there were adaptational trends. Perhaps the discussion can be outlined in a diagrammatic way as follows (table 1).

Evolutionary Rates of the Ceratopsia

Among the dinosaurian suborders the Ceratopsia were the most limited in their time range, being restricted to the upper part of the Cretaceous period. The ankylosaurs were almost as restricted, but their evolutionary history did extend throughout the full extent of Cretaceous times, while the other suborders persisted through at least parts of two Mesozoic periods, and in some cases, through the entire range of the Mesozoic era. A comparison of the time ranges in the six recognized dinosaurian suborders can be shown in tabular form.



A broader comparison will show that the ceratopsians were not only a short-lived suborder of dinosaurs, but also a short-lived group of reptiles. In the entire history of reptilian evolution there are few groups of subordinal rank with so restricted a time range. Moreover in other restricted groups, the restriction is more apparent than real, generally being due to the inadequacy of the fossil record rather than to the brevity of the phylogenetic history. Such, for instance, is true with regard to the eunotosaurs from the Permian of South Africa, known from a single genus, or to the mesosaurs from the Lower Permian of South Africa and South America, known from three genera. Our knowledge of ceratopsian evolution, on the other hand, is fairly complete, and while future discoveries may fill in many details it can safely be said that they will not extend the geologic range of the group to any appreciable extent.

As a matter of comparison, among the persisting reptiles, pleurodire and cryptodire turtles date back to Cretaceous and Jurassic times respectively, the eusuchian crocodiles to the Jurassic, the rhynchocephalians to the Triassic, and the lizards and snakes to the Cretaceous. There is reason to think that the history of the lizards and snakes extends back into Jurassic times.

This means that evolutionary rates in the ceratopsian dinosaurs were rapid, even allowing for the fact that this is a group in which the amount of evolutionary development was rather limited. Perhaps this fact can best be illustrated by comparing the evolution of size, as measured by total length in the ceratopsian dinosaurs and in the other lines of dinosaur evolu-

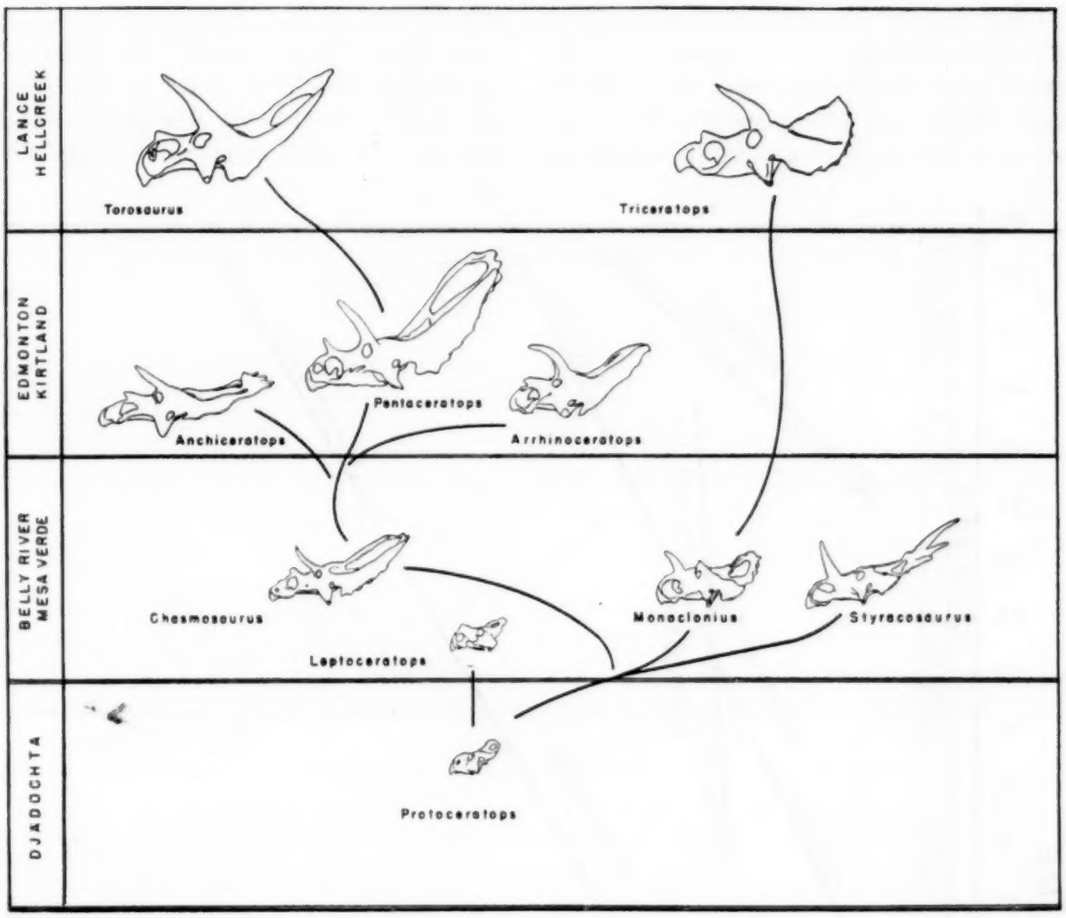


FIG. 3. Adaptive radiation of the Ceratopsia, as shown by evolution in the skull. The evolutionary line to the left is that of the long-frilled ceratopsians, the one to the right, that of the short-frilled ceratopsians. Modified from Lull, 1933. All figures approximately to the same scale.

tion, with duration of geologic time. This is shown by the graph, figure 4.

In this chart it can be seen that the Ceratopsia progressed from adult animals having lengths of about two meters to adult animals having lengths of about seven meters, and this size increment took place within the 15 or 20 million years that is here assigned to the upper part of the Cretaceous period.

In contrast with this, the ornithopod dinosaurs showed a similar size increment that extended over a period of time about three times the length of that required for the entire evolution of the ceratopsians. The armored dinosaurs, being relatively slowly evolving types at least so far as increase in size is concerned, showed a very small increment in a period of time that was roughly twice the length of ceratopsian evolutionary history, while the stegosaurs or plated dinosaurs also showed a smaller size increment occupying a greater time lapse than is seen in the ceratopsians. The theropod dinosaurs showed a length increment of from two to 14 meters in the time interval between the upper Triassic and the end of the Cretaceous, a large size increase but at a rather moderate rate, since a greater part of the Mesozoic period was involved in its completion. The sauropod dinosaurs showed a size increment of from about six meters in the upper Triassic to 18 meters or more in the upper Jurassic, an evolutionary rate that is, interestingly enough, closely parallel to that for the ceratopsians.

This comparison of evolutionary rates in the six suborders of dinosaurs is concerned with total length only. It would be desirable to have other quantitative comparisons, but such comparisons would be difficult to obtain. For instance, a comparison of body masses would be enlightening, and if it could be made with any degree of certainty would be more indicative of evolutionary rates in the dino-

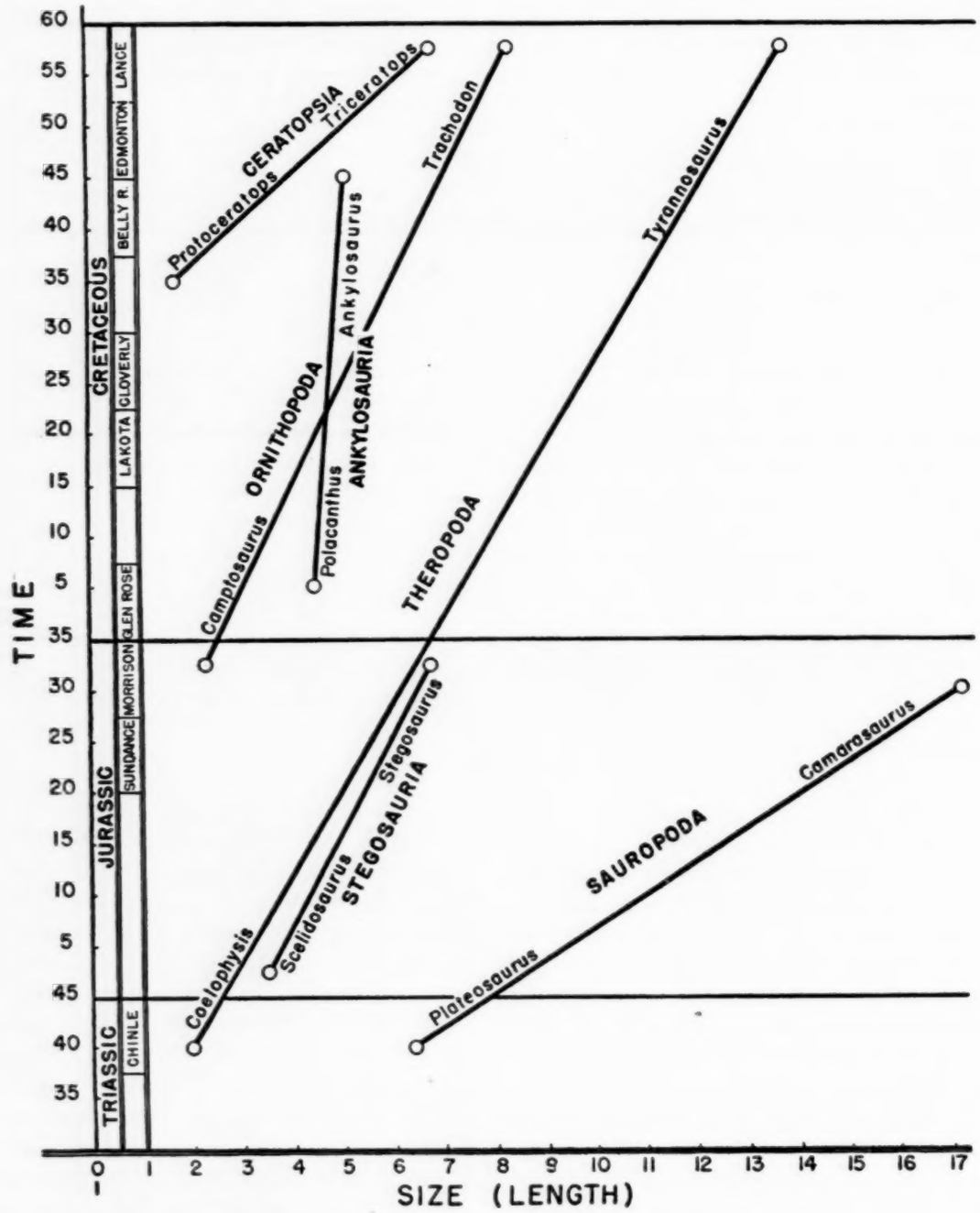


FIG. 4. A comparison of evolutionary rates, as based upon total lengths, in the suborders of dinosaurs. In each suborder a straight line connects an early, primitive genus and a late, specialized genus, thus giving an approximate indication of the average evolutionary rate for the suborder. The more nearly horizontal the line, the higher the rate of evolution as regards size increase. Time is in millions of years, size in meters. Characteristic formations in the North American Mesozoic sequence are shown.

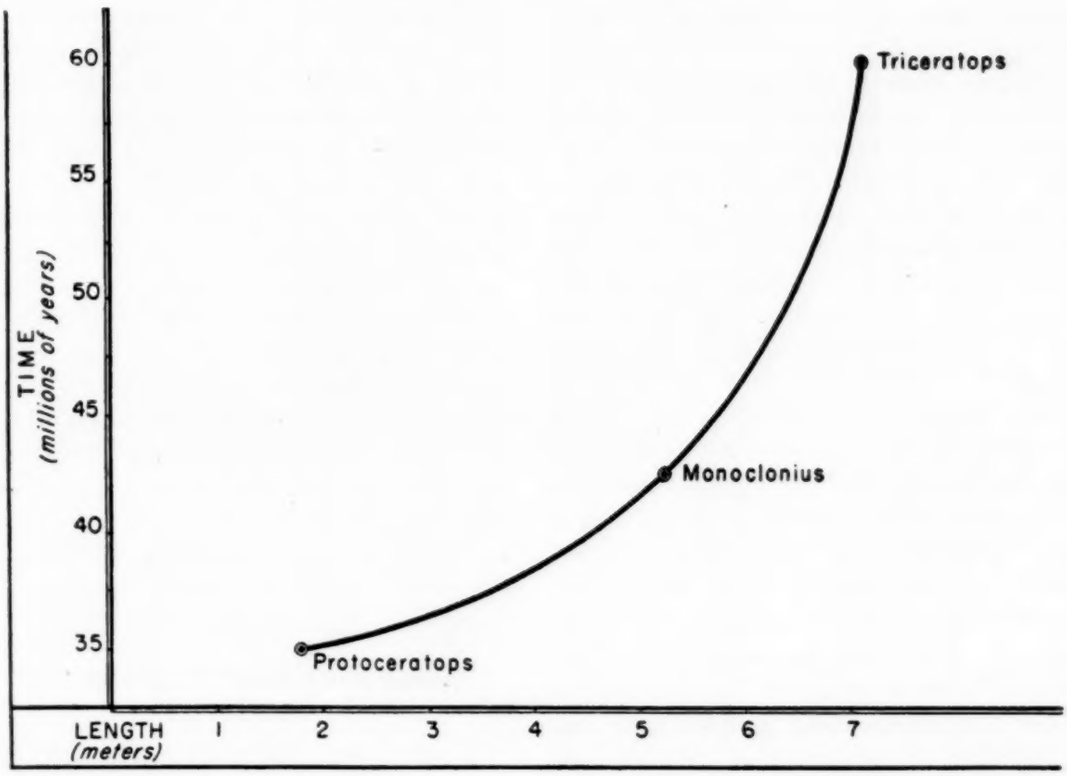


FIG. 5. The evolutionary rate, as based upon total lengths, in the phylogenetic line from *Protoceratops* (Djadochta) through *Monoclonius* (Belly River) to *Triceratops* (Lance).

saurs than the comparison of length. But such a comparison would involve estimates of body weights in each case, and would thus be subject to a large degree of error. To carry the comparisons down to individual parts of the body, such as the skull, or the legs, is virtually impossible, because of the highly varied and different adaptations in the dinosaurs that make direct comparisons like these almost useless. Even this simple comparison of lengths must not be taken too literally. For instance, the assignment of time durations within the Mesozoic periods are rather arbitrary, and this fact must be kept in mind. Moreover, the representation of evolutionary rates as straight lines connecting in each case a small early representative of each suborder with a large late form is not strictly correct. Where we have the evidence of intermediate forms, such as in the ceratopsians or the theropods, we know that evolution in size was comparatively rapid during the first part of the sequence, and relatively slow during the later phases of phylogenetic history. But since intermediate forms are not known in all of the phylogenetic lines under consideration, this method of showing merely early and late representatives connected by a straight line is used to indicate the average rate of evolution.

In this connection it may be interesting to attempt an analysis of the evolutionary rate of length increment within the phylogenetic sequence running from *Protoceratops* through *Monoclonius* to *Triceratops*. This sequence, as pointed out above, probably represents a valid evolutionary line, and it is a sequence in which complete skeletons of the genera concerned are well known.

If skeletal lengths of typical examples of the three genera named above are plotted against their approximate positions in Cretaceous time, a curve—not a straight line—is obtained. This curve represents the rate of increase in total length in the short-frilled group of ceratopsians through geologic time, and it shows that in the

earlier phases of the phylogenetic history of these animals there was a rapid increase in length, while in the later phases of the history the rate became appreciably slowed down. Thus, *Monoclonius* which probably was not far removed from *Protoceratops* in time, was many times larger than the Mongolian genus, whereas *Triceratops*, probably separated from *Monoclonius* by a considerable time lapse, was not a great deal larger than this latter genus.

The shape of the curve is, of course, governed by the assumptions made as to relative lengths for the various segments of geologic time involved in the comparison, namely those time lapses during which the Djadochta, Belly River, Edmonton and Lance formations were deposited. But upon the basis of any reasonable assumption as to the duration of upper Cretaceous time, founded upon our knowledge of stratigraphic relationships in the several continental areas, it seems logical to suppose that some sort of a differential rate of increase in this phylogenetic line will be the result.

There is nothing surprising in this; indeed, the picture of a rapid increase in size during the earlier phases of evolutionary history in the *Protoceratops—Triceratops* line followed by a distinct slowing down of size increase during the later portions of the sequence, is in line with what we know about many other examples of phylogenetic history. While a more or less constant rate of evolution is frequently found in the study of phylogenies as based upon fossil materials, it is not at all uncommon to find lines in which evolutionary rates show profound differences at different stages of geologic time. We often see a phylogenetic line evolving very rapidly during the early phases of its history, only to slow down, and at times to become almost static, once it has become well established.

The ceratopsians as a group provide an example of this phenomenon. We do not know ceratopsian history with any degree of certainty prior to the appearance of *Protoceratops*. It would seem probable, however, that the basic transitions from a generalized ornithischian dinosaur to the primitive ceratopsian stage as represented by *Protoceratops* were made with great geologic rapidity; in other words, there was a period during which quantum evolution established the ceratopsian adaptational pattern. From *Protoceratops* the development of specialized ceratopsian adaptations was also rapid; not much time was involved in the transition from a small, hornless ceratopsian to a giant, horned ceratopsian. After this last stage was attained, however, evolution was comparatively slow, and, as pointed out above, it involved mainly a limited increase in size and various adaptational changes in the structure of the skull.

Geographic Limitations of the Ceratopsia

Why should the Ceratopsia, with the exception of *Protoceratops*, be confined to the continent of North America? Does this represent a condition that prevailed during the upper part of the Cretaceous period, or is the limitation of the ceratopsians to North America, as based upon our present information, more apparent than real, being the result of accidents in preservation with a resultant imperfect knowledge of the fossil record? Let us turn first to the problem of absences of ceratopsians in the fossil record, and their significance.

The remains of *Protoceratops* in the Djadochta formation of Mongolia constitute abundant evidence as to the presence of ceratopsians in Asia during the opening phases of upper Cretaceous times. But beyond *Protoceratops* our published information as to the presence of the Ceratopsia in Asia is limited to a single fragment, identified by Gilmore some 15 years ago as the epoccipital from the frill of a *Pentaceratops*—like dinosaur. This is indeed slender evidence, but slight as it is, it appears to be valid. The bone was found at Baiying Bologai, Mongolia, a locality of which the geologic horizon has

never been accurately determined. It may be later than the Djadochta in time, but if so it represents our first inkling as to Cretaceous sediments that were laid down in Mongolia subsequent to the deposition of the Djadochta formation. All of the other Cretaceous horizons described are as old as or older than the Djadochta.

Thus we find ourselves against a blank wall in an effort to follow the later history and distribution of the Ceratopsia in Asia. To date, the Djadochta formation is the latest Cretaceous formation in Mongolia containing an identifiable fauna, and this yields the most primitive of the ceratopsians. It is quite possible that ceratopsians were present in northeastern Asia in the later phases of the Cretaceous period, but this is a question that will have to wait on future discoveries for its solution.

While the future discovery of later Cretaceous ceratopsians in Asia is here considered as probable, the discovery of these animals in the upper Cretaceous sediments of Europe is here considered as unlikely. Upper Cretaceous dinosaur-bearing beds are now known in various parts of Europe, and although these sediments carry remains of various other suborders of dinosaurs, there are no evidences in them of ceratopsians. Similarly, the upper Cretaceous dinosaur-bearing sediments of Africa, so far as they are known, do not reveal the presence of ceratopsians in their contained faunas. Therefore, the absence of ceratopsians in the upper Cretaceous of Europe and of Africa is regarded as representing a probable real absence of these animals at that time, rather than an imperfection of the fossil record, as is very likely the case in northeastern Asia.

Turning now to South America we find one ceratopsian, described by von Huene upon the basis of a fragment of a mandible. But this specimen is so poorly preseved that its assignment to the Ceratopsia cannot be considered as beyond question. Consequently the presence of ceratopsians in the upper Cretaceous of South America must at the present time be regarded as a debatable point. It may be the result of imperfections in the fossil record, or it may be a real absence.

So we see that the Ceratopsia were, in the light of our extant knowledge, essentially a North American group of reptiles. They very possibly were present in northeastern Asia in uppermost Cretaceous times, but this is at the present time mere speculation. They very probably were not present in Europe or Africa, and probably not in South America, either. Granting, then, for the sake of the present consideration, that the ceratopsians above the evolutionary level of *Protoceratops* were confined to North America, what can we deduce from their geographic distribution in this region?

In North America the ceratopsians are known at the present time from the western Great Plains and Rocky Mountain regions, the localities at which these reptiles have been collected being contained within an area including Alberta, Saskatchewan, Montana, the Dakotas, Wyoming, Colorado, New Mexico, western Texas and Coahuila. Within this area are most of the continental upper Cretaceous exposure in North America. Therefore, it seems evident that discoveries of ceratopsian dinosaurs in North America have been limited to the regions listed above primarily because of the limitations of the areas of exposures in which such dinosaurs might well be expected. Now it is an interesting fact that other upper Cretaceous dinosaurs have been found in scattered localities outside of the Great Plains–Rocky Mountain region. For instance, hadrosaurs have long been known from the Cretaceous of New Jersey, and recently hadrosaurian remains have been excavated in California. It must be remembered, however, that the hadrosaurs were semiaquatic dinosaurs and their fossils are to be expected in beds of marine origin where the fossils of upland ceratopsians would not be preserved. It is certain that the hadrosaurs found in New Jersey come from a

marine facies, probably an off-shore deposit, and the same may be assumed for the material from California.

Therefore it might be assumed that the absence of ceratopsians from the Cretaceous of New Jersey, for instance, is the result of the imperfection of the record—that these off-shore marine sediments have yielded hadrosaurs because the hadrosaurs were water-loving dinosaurs, and have not yielded the remains of ceratopsians because the horned dinosaurs were upland forms. But as against this assumption is the fact that certain carnivorous theropods have been found in the Cretaceous of N. Jersey and these were upland dinosaurs as were the ceratopsians. Is it possible, then, that the absence of ceratopsians from the Cretaceous of eastern North America represents a real absence of these animals from this region during upper Cretaceous times? Is it possible that the confinement of the ceratopsians to the western Great Plains—Rocky Mountain area represents more or less the actual distribution of these dinosaurs during the geologic ages in which they were living?

According to paleogeographic evidence it would seem that an arm of the sea extended from the gulf region northward through the western Great Plains area during upper Cretaceous times. During the later phases of the upper Cretaceous period, at a time about equivalent to that of Belly River sedimentation, this sea arm or embayment was rather large, extending far north into Canada and to the east over the northern Great Plains states. By the end of Cretaceous times, however, during the period of Lance sedimentation, this sea arm had diminished to a narrow trough extending northwardly through eastern New Mexico and Colorado and western Nebraska and the Dakotas. It

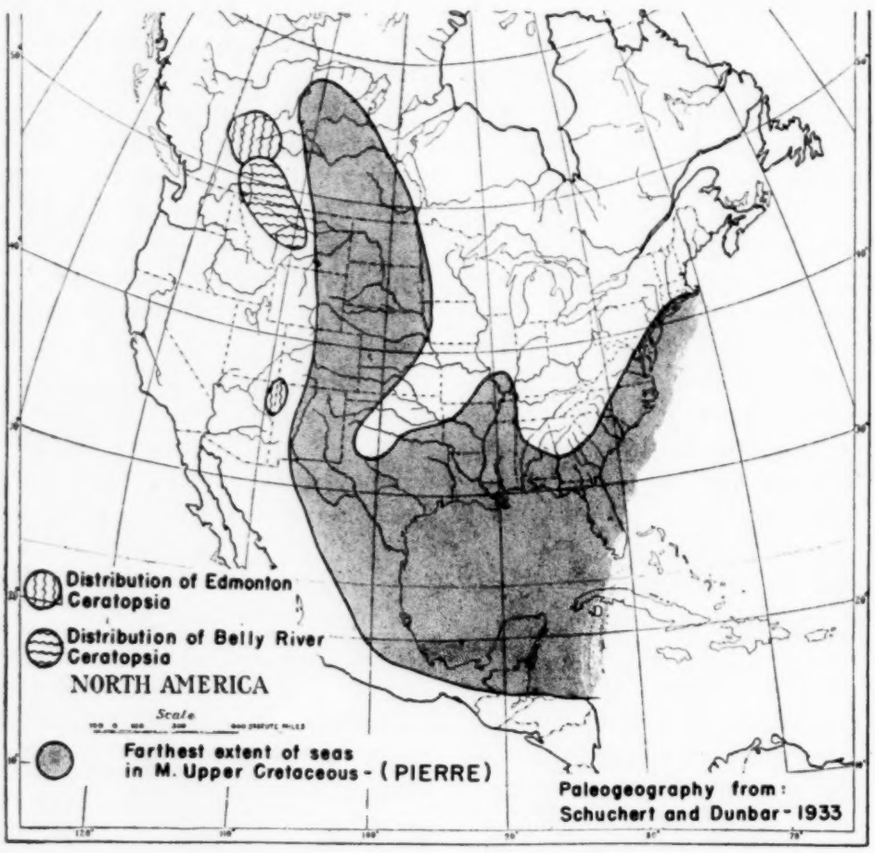

Distribution of Edmonton Ceratopsia
Distribution of Belly River Ceratopsia
NORTH AMERICA
Scale
Farthest extent of seas in M. Upper Cretaceous - (PIERRE)
Paleogeography from: Schuchert and Dunbar - 1933

FIG. 6. The known distribution of Belly River and Edmonton ceratopsians and the extent of the Pierre Sea, in middle Upper Cretaceous times.

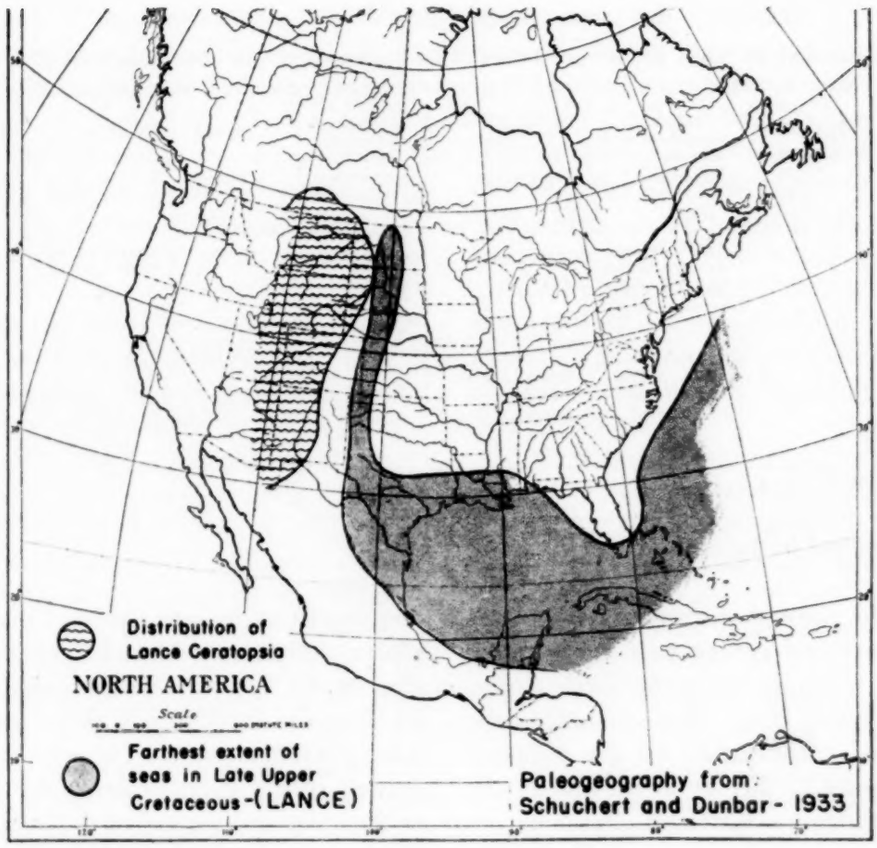


FIG. 7. The known distribution of Lance ceratopsians and the extent of the Lance (Cannonball) Sea, in late Upper Cretaceous times.

barely crossed the Dakota border into Saskatchewan and Manitoba.

Now it is interesting to see that the sediments in which ceratopsians have been discovered lie along the western border of this epeiric seaway, in regions that during upper Cretaceous times were continental areas. None of the ceratopsian-bearing sediments are to be found to the east of the marine incursion.

Is it not possible, therefore, that the upper Cretaceous sea formed a barrier to the eastward spread of the ceratopsians? If it is assumed that the presence of *Protoceratops* in Mongolia indicates a northern Asiatic center of origin for the ceratopsians, then it can further be assumed that during upper Cretaceous times these dinosaurs migrated or spread from their Asiatic point of origin to the east, across the Bering region and down into western North America, from whence they were prevented from extending their range directly eastward by the sea barrier, and to the northeast, around the upper end of the seaway, by adverse climatic conditions. On the basis of the known facts, such as a conclusion appears to be logical.

In this connection it is interesting to note the known distribution of the ceratopsians in North America in Belly River, Edmonton and Lance times, respectively (table 2). In the Belly River, the horned dinosaurs are confined to an area in southern Alberta and northwestern Montana. In the Edmonton, these animals are found in Alberta, generally to the north of their Belly River distribution, and also in rocks of comparable age in New Mexico. In the Lance the ceratopsians are widely spread, from the Canadian border and Montana in the north, southwardly through the Dakotas, Wyoming, Colorado and New Mexico. Does this sequence

TABLE 2. *Geographic and geologic distribution of the Ceratopsia*

Genera contained within a square are believed to have existed simultaneously in the same area.

	Mongolia	Alberta Saskatchewan	Montana N. Dakota	Wyoming S. Dakota	Colorado	N. Mexico	Texas Mexico
Lance Hell Creek Ojo Alamo		*Triceratops*	*Triceratops*	*Triceratops* *Torosaurus*	*Triceratops*	*Triceratops* *Monoclonius*	(Ceratopsian)
Edmonton Kirtland		*Anchiceratops* *Arrhinoceratops* *Monoclonius* *Leptoceratops*				*Pentaceratops* *Monoclonius*	
Belly River		*Chasmosaurus* *Styracosaurus* *Monoclonius* *Eoceratops**	*Styracosaurus* *Monoclonius* *Brachyceratops** *Leptoceratops* *Ceratops**				
Djadochta	*Protoceratops*						

* Not discussed in this paper.

indicate the spread during geologic time from a northern center to a wide north and south range in western North America? Probably not. For instance, the presence of ceratopsians in the Edmonton sediments to the far north and in the contemporaneous Kirtland deposits in New Mexico would seem to indicate that the apparent restriction of horned dinosaurs to these two areas is the result of geologic processes which have resulted in the elimination of fossiliferous rocks of this age in the intervening regions. In other words, it is reasonable to think that the distribution of Edmonton ceratopsians, and of Belly River ceratopsians before them, was continuous along the western border of the upper Cretaceous seaway, as from the evidence we know it was during Lance times.

It is realized, of course, that in this discussion different conclusions are being drawn from negative evidence. On the one hand, it is postulated that the lack of ceratopsians in the eastern Cretaceous is probably the result of a real absence of these animals from this region during Cretaceous times. On the other hand, it is suggested that the small areas in which Belly River and Edmonton ceratopsians are now found are the result of geologic processes, and that these animals were once present in a continuous range running north and south through the western Plains and Rocky Mountain region, as is true of the Lance ceratopsians. But it is felt that the facts justify these arguments. The presence of the upper Cretaceous seaway offers good evidence for a barrier to the eastward spread of the ceratopsians. The continuous range of the Lance ceratopsians along the western border of the sea suggest that similar relationships held during the preceding ages, when the Edmonton, and before them, the Belly River ceratopsians were living.

AN INTERPRETATION OF CERATOPSIAN EVOLUTION

We have so far reviewed the evolution of the ceratopsian dinosaurs in several of its aspects. Thus we have considered the problem of adaptive radiation or the evolutionary pattern within this suborder of reptiles, the problem of evolutionary rates as seen in these long-extinct animals and the problem of the geographic limitations of the ceratopsians during the course of their evolution. Interpretations of these several problems have been set forth in connection with each of them. At this place it may be useful to attempt a broader interpretation of ceratopsian evolution, based upon the varied facts and their interpretations offered in the preceding discussion.

In the first place, it must be realized that, by and large, size increase is a constant throughout the evolutionary history of the ceratopsians. With the exception of the genus *Leptoceratops*, all of the horned dinosaurs after *Protoceratops* were large animals, and they were large to about the same degree of largeness. We know that there were certain size differences in the adults of the various ceratopsian genera, but generally speaking they all were animals on the order of about 20 feet in length, with their other proportions corresponding; consequently, it is proper to say that the ceratopsians all showed a size increase during evolution of about the same degree of magnitude.

Moreover, as pointed out on a preceding page of this discussion, the ceratopsian dinosaurs were all pretty much alike as regards the post-cranial skeleton. Indeed, a study of the osteology of these forms will show that the differences between the various genera, so far as the skeleton behind the skull is concerned, were differences in details of morphology. They were all adapted along the same structural pattern that was first established by *Protoceratops*.

Therefore, in studying the adaptive radiation of the ceratopsians, we see that lines of phylogenetic differentiation are to be recognized mainly on the basis of horn and frill patterns. All of the ceratopsians had frills, but the frills differed from genus to genus. All of the ceratopsians above the level of *Protoceratops* had horns, but here again, the horns differed from genus to genus. What is more, genera differing from each other by reason of their horn and frill structures were contemporaneous. Therefore, we are led to the conclusion that selection pressures during ceratopsian evolution did not favor one pattern of horns and frill to the exclusion of others, but rather that once the survival value of horns and frill had been established, these could develop in a variety of ways. A ceratopsian with large brow horns, a small nasal horn and a fenestrated frill could live side by side with a genus characterized by similar horns, but with a solid frill, and both of these could be contemporaneous with a type having a fenestrated frill, but differing from the others by virtue of a very large nasal horn and reduced brow horns. It would seem as though horns and frill as such had a high adaptive value, the horns serving for defense, the frill as an attachment for large muscles that gave great power to the thrust of the horns. But, as we have seen, the pattern or combination of horns and frill might vary from genus to genus.

Is it not reasonable to suppose, therefore, that the various forms of horns and frill in the ceratopsians were the result of random mutations, not suppressed by selection? And if this be so, is it not possible that these mutations became established as a result of comparative isolation in small populations?

We have seen that the large, specialized ceratopsians seemingly were limited to North America, and how, in this continent, there is reason to think that they were confined to the western regions, west of the upper Cretaceous seaway. Of course, a range that stretches from New Mexico into Alberta is not particularly limited, but on the other hand this is not an extensive range for large terrestrial vertebrates such as the ceratopsians. Therefore, it is logical to suppose that in the early stages of ceratopsian evolution, perhaps after these animals had migrated into the North American continent from Asia, there were established several geographic centers more or less isolated from each other. The ceratopsians developed in these centers, and since populations were relatively small, mutations could be established and spread with comparative speed by a process of evolutionary drift through these limited populations. It may be supposed that subsequently these isolated and differing populations expanded, with a resultant coexistence of differing genera, mutually tolerant to each other. Such is the hypothetical picture as here suggested upon the basis of our

knowledge of ceratopsian evolution and distribution.

It may be that we can see a modern parallel to the ceratopsian dinosaurs in the African antelopes. Like the Ceratopsia, the antelopes of Africa have evolved very rapidly, geologically speaking. Like what is here presumed for the Ceratopsia, these antelopes are for the most part limited to a single continental area. And like the Ceratopsia, the African antelopes show a variety of adaptations in certain characters (particularly the horns) that seem to be of equal selective value. Thus, in the antelopes the ability to run fast and the possession of horns are of primary importance for survival. But the form of the horns seems to be of secondary importance, so we find various genera, characterized by widely differing horn structures, living together successfully in the same environment.

An example of the variety of horn structure to be found in a single subfamily of African Bovidae is to be seen in the Hippotraginae. In this assemblage are included the sable antelope, *Hippotragus,* with the horns recurved posteriorly; the oryx, *Oryx,* with long, straight horns; the addax, *Addax* with the horns openly spiral; the water buck, *Kobus,* the puku, *Adenota* and the lechwe, *Onotragus,* with recurved horns, laterally divergent; the reedbuck, *Redunca,* with the tips of the horns curved forwardly; the blesbok, *Damaliscus,* with short, simple horns; the rhebok, *Pelea,* with slightly recurved, spike-like horns; the gnus, *Connochaetes* and *Gorgon,* with the horns curved down and out and then up; and the hartebeest, *Alcelaphus,* with horns something like those of the gnu, but more complexly curved in their distal regions. Here is a variety of horn development much greater than that to be found in the ceratopsians, having evolved in genera many of which now have contiguous or overlapping distributions.

It must be admitted that, even though limited to one continent, the populations of many genera of African antelopes are now very large. We know from the fossil evidence, however, that the present African antelope fauna had its origins during Pliocene times to the north, in the Mediterranean region. And it is possible that, during the relatively brief geologic time when the various phylogenetic lines of antelopes were becoming established, there were comparative isolated centers of development in which the determining mutations were taking place.

Whether these suppositions are valid or not, we do know the end results in the modern antelope fauna of Africa, an assemblage of closely related genera that show certain parallels in their evolution to what we see in the ceratopsian dinosaurs.

Summary

In this discusion of Ceratopsian evolution certain factors in the phylogenetic development of the horned dinosaurs have been stressed. The adaptive radiation of the Ceratopsia has been outlined, particularly as it is concerned with the phylogenetic development of the skull; and problems of evolutionary rates in these dinosaurs, as compared with other dinosaurs have been considered. Moreover, the probable geographic distribution of the Ceratopsia during upper Cretaceous times has ben elucidated, and reasons to explain this distribution have been suggested.

Upon the basis of what we know as to the phylogeny and distribution of the ceratopsian dinosaurs, it is suggested that these animals probably went through the early stages of their evolutionary development as small populations, limited to the western part of North America. Random mutations affecting the form and development of the horn cores and the frill took place in these small populations, with the result that several phylogenetic lines, characterized by different skull patterns, were quickly established. Since the skull patterns so evolved had equal survival values, the phylogenetic lines of which they were respectively characteristic con-

tinued through the upper part of the Cretaceous period. Moreover, since the original limited populations probably expanded, it would appear that the genera typical of the various lines of ceratopsian evolution became established side by side in ranges that were contiguous or probably to a large degree overlapping. They were mutually tolerant, and it is likely that there was no great amount of competition between them. So established and so living together, the various ceratopsians continued through the last and the final phases of the Cretaceous period, to become extinct, along with all of the other dinosaurs, during the transition from Mesozoic to Cenozoic times.

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THE ORIGIN OF A MAMMALIAN ORDINAL CHARACTER

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INTRODUCTION

By studying the evolutionary trends of organisms paleontologists have become aware of the peculiar circumstances surrounding the origin of higher categories. Most orders, classes and phyla of invertebrates and vertebrates appear abruptly in the geological record with one or more character complexes well differentiated but without any indication of transitional stages. Several theories have been postulated to explain this phenomenon but there have been few detailed discussions of particular examples. This paper represents an attempt to analyze the evolutionary trend culminating in the appearance of an order of mammals, the even-toed ungulates or Artiodactyla.

Of the twenty-six currently recognized orders of eutherian mammals, about fifteen probably had a Paleocene origin. The identification of the earliest members of an order is dependent upon the possibility of identifying one or more definitive ordinal character complexes, which are usually present in an otherwise still relatively primitive stock. The determination of the ancestral group from which a mammalian order such as the Artiodactyla originated is, by necessity, largely based on inference. Usually but a few heritage characters are available that indicate definite affinity and thus tend to bridge, however incompletely, the structural, if not the chronological hiatus.

The first known members of the Artiodactyla are possibly unique among the mammals in that they can be identified positively only on the basis of a single character complex, in the foot, which practically reached its definitive form before other skeletal characters were in more than an incipient stage of phylogenetic development. The intermediate steps in the evolution of this complex, which represents the highly specialized form of the tarsus, are unknown. The primitive generalized (or relatively unspecialized) type from which it evolved can be recognized, however, and the time interval during which the transformation took place can be estimated with reasonable accuracy. It is possible, therefore, to consider the magnitude of the morphological change during this period as well as the associated functional alternations. In discussing these problems here it will also be of interest to consider possible factors that favored an initial emphasis on the evolution of this particular character complex. A more detailed study of the origin and function of the artiodactyl tarsus has been published elsewhere (Schaeffer, 1947), and only such details of morphology and function as are necessary for the understanding of the problem will be repeated.

The erection of the Cohort Ferungulata (Simpson, 1945) to include the various orders of extinct and Recent carnivores and ungulates (fig. 1) is based on the fact that these greatly diversified groups had a common late Cretaceous origin. The paleontological data suggest that the most primitive ferungulates, the arctocyonid creodonts, reached their definitive status before the beginning of the Paleocene. Likewise the earliest ungulates, the condylarths, were differentiated by the early Paleocene.

Until recently, the ancestral stock of the Artiodactyla was essentially unrecognized although the condylarths as a group were considered to be structurally antecedent. Simpson (1937) has pointed

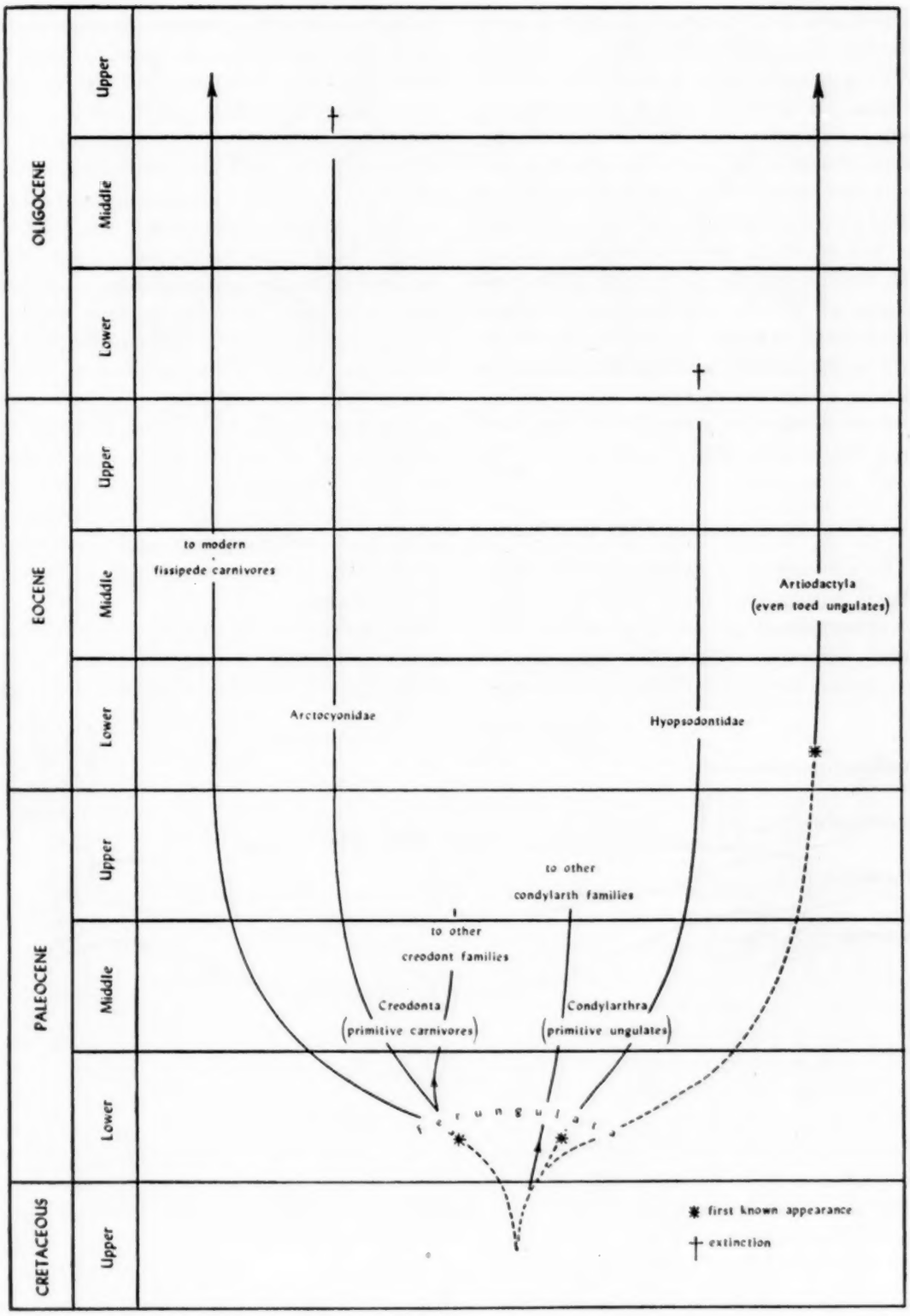

FIG. 1. Simplified phylogeny indicating the relationship of the Artiodactyla to the other ferungulate groups mentioned in the text.

out, however, that the dentition of the earliest and most primitive family of condylarths, the Hyopsodontidae, is almost indistinguishable from that of the earliest artiodactyls such as the Lower Eocene genus *Diacodexis*. This resemblance, Simpson states, is much too great in the significant details of tooth form to be ascribed to convergence. In fact, one genus now placed in the Hyopsodontidae was at first considered to be a true Paleocene artiodactyl on the basis of tooth form. The available fossil evidence, therefore, leads to the almost inescapable conclusion that the evolutionary trend which culminated in the Order Artiodactyla was initiated no earlier than sometime in the Lower Paleocene.

Paleontological Evidence

The skeleton of a hyopsodontid condylarth is similar in many respects to that of a generalized placental mammal, possessing primitive characters that are, in fact, common to the earliest representatives of several orders. Because of this basic resemblance, various hyopsodontids have previously been assigned to the Artiodactyla, the Primates and the Insectivora. Recent studies, particularly on the dentition, indicate affinity with the Condylarthra (as well as relationship with the Artiodactyla). It might be pointed out here that tooth characters are used extensively in paleomammalogy, not only to determine the relationships of higher categories, but also to separate taxonomic groups at generic and specific levels. Although there are examples of parallelism and convergence in tooth form among mammals, the chances of close duplication of a complicated tooth pattern are so exceedingly remote in distantly or unrelated groups that the dentition, in most cases, offers a more exact indication of relationship than almost any other part of the skeleton.

In contrast to the dentition, the hyopsodontid foot (fig. 2), as preserved in the genus *Chocroclaenus*, is structurally un-

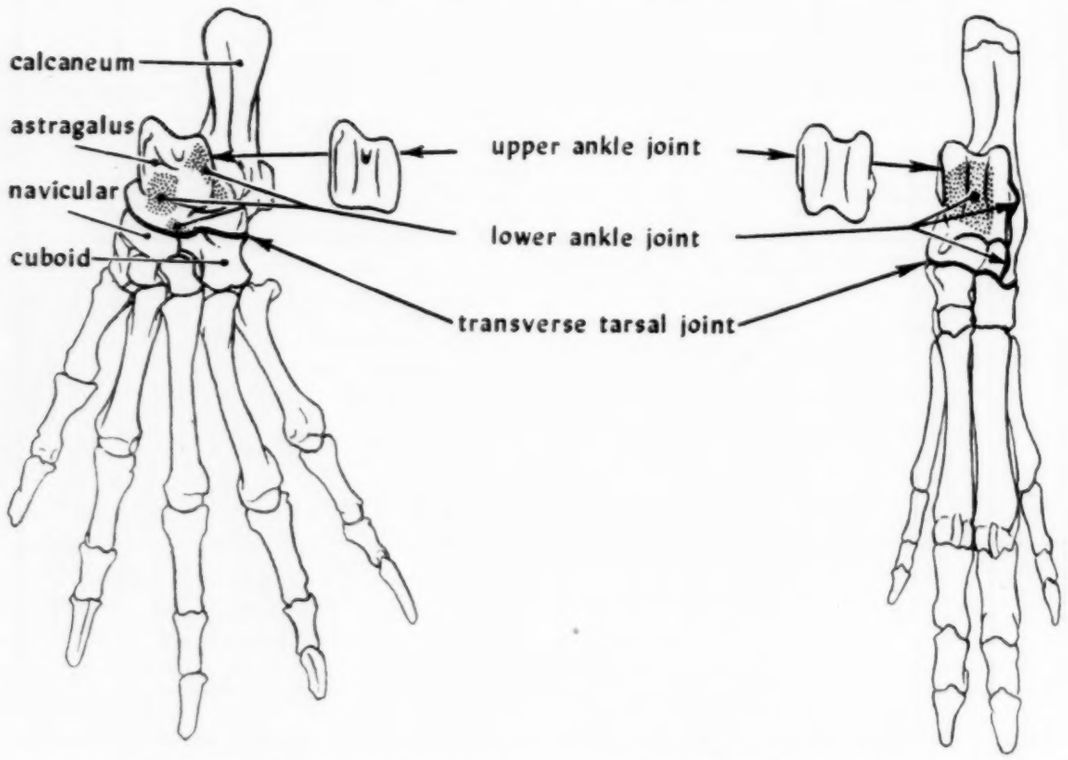

Fig. 2. Comparison of the left hind foot of a primitive ferungulate (*Claenodon*) and an artiodactyl (*Sus*) showing the location of the three main tarsal joints. The stippled areas represent the articulations between the astragalus and the calcaneum.

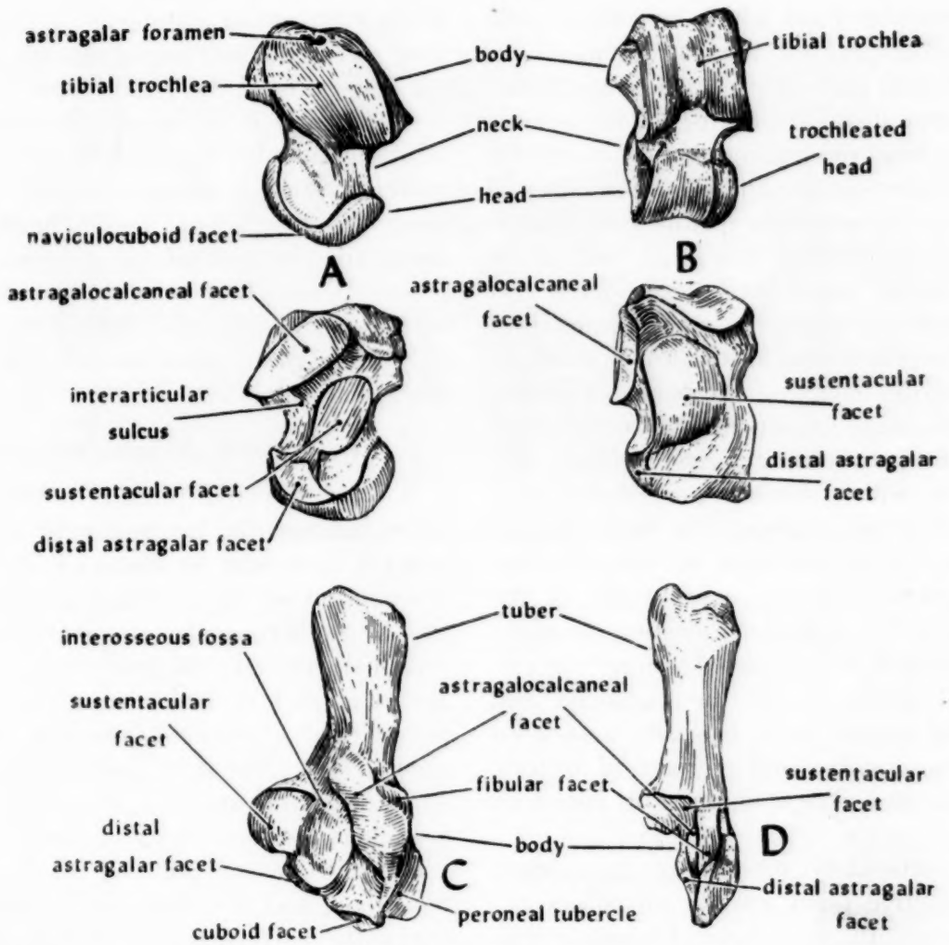

FIG. 3. Dorsal and ventral views of the astragalus of the hyopsodontid Condylarth *Choeroclaenus* (A) and the artiodactyl *Diacodexis* (B) and dorsal views of the calcaneum of arctocyonid creodont *Claenodon* (C) and the artiodactyl *Merycochoerus* (D).

changed from that of the arctocyonid creodonts, including the presence of claws rather than hoofs (hoofs are present in all other condylarth families). Among the bones of the foot, the astragalus and calcaneum, which are the proximal elements of the tarsus proper, most readily demonstrate different types of locomotor adaptation. Matthew (1909 and 1937) considered the mammalian astragalus to be of almost as great diagnostic value as the dentition, although others have demonstrated that it must be used with caution (Simpson, 1937).

The astragalus of *Choeroclaenus* (fig. 3A) has a wide, shallow trochlea for articulation with the tibia. The head of the astragalus, which contacts distally both the navicular and the cuboid bones, is mediolaterally rounded. The neck between the tibial trochlea and the head is constricted. The plantar surface of the astragalus has an elongated, ovoid astragalocalcaneal facet which is separated from an oval sustentacular facet by a deep interarticular sulcus. A small, poorly defined articular surface, which may be called the distal astragalar facet, is situated adjacent to the naviculocuboid facet.

The calcaneum of *Choeroclaenus* (fig. 3C) has a strongly developed heel process or tuber. The astragalocalcaneal facet of this bone is located at the proximal end of the tuber, with a similarly shaped fibular facet adjacent to its medial border. There is a well-developed shelf or sustentaculum on the lateral side of the cacaneum, on the dorsal surface of which is situated the

sustentacular facet which articulates with its counterpart on the astragulus. The rhomboidal cuboid facet makes up almost the entire distal surface of the calcaneum.

This brief description of the two proximal elements of the eutherian tarsus could apply to the primitive members of a number of mammalian orders as well as to many more specialized descendants. It would fit the astragalus and calcaneum of such diverse forms as the less specialized insectivores, many of the primates including man, some rodents and most terrestrial carnivores. With relatively minor differences, which Matthew nevertheless considered of importance, this basic pattern has been very persistent in spite of adaptive trends affecting other parts of the skeleton. The greatest alteration, as might be expected, has occurred among the terrestrial mammals in the cursorial and saltorial types. It is basically associated with two interrelated mechanical factors, increase in leverage, increase in speed, or both.

The artiodactyl tarsus (fig. 2) reached its definitive form, except for minor refinements, in the early Eocene. The highly characteristic astragalus (fig. 3B) has a deepened tibial trochlea with sharp medial and lateral crests. A distinct neck region is no longer evident. The portion of the head articulating with the cuboid and navicular bones has been transformed into an anteroposteriorly rounded trochlea with flattened medial and lateral surfaces. The plantar surface of the astragalus is dominated by the sustentacular facet which is elongated parallel to the long axis of the entire bone. The astragalocalcaneal facet has been reoriented in the same manner. The distal astragalar facet on the lateral surface of the trochlea is more clearly defined and is of greater functional significance.

The artiodactyl calcaneum (fig. 3D) has a relatively less robust tuber and a greatly modified body. The sustentaculum has been altered so that its facet is directed more distally than dorsally, while the astragalocalcaneal and fibular facets, in their astragalar counterparts, have their long axes oriented essentially parallel to the long axis of the entire bone.

The change in the form of the distal end of the astragalus was associated with an increase in the articular contact of this bone with the cuboid and a marked decrease in the area of the calcaneocuboid articulation. The proximal surfaces of both the navicular and cuboid are markedly concave to accommodate the distal astragalar trochlea.

Functional Interpretation

A more dynamic picture of the differences between the hyopsodontid and artiodactyl tarsi may be obtained through a comparison of the orientation and function of the three major tarsal joints. For practical reasons, the positions of these axes were determined for the tarsi of the arctocyonid creodont *Claenodon* and the sheep, *Ovis*. The three joints (figs. 2 and 4) in question are (a) the upper ankle joint between the tibia and fibula on one side and the astragalus and calcaneum on the other, (b) the lower ankle joint between the astragalus and calcaneum and (c) the transverse tarsal joint between the astragalus plus the calcaneum and the cuboid plus the navicular.

In mammals generally, the upper ankle joint has probably had a more conservative history than either the lower ankle or transverse tarsal joints. The orientation of the axis is roughly at right angles to the long axis of the tibia and runs in a mediolateral direction. Motion at this joint is always restricted to an anteroposterior movement (dorsi-and plantar flexion) of the foot on the lower leg. In the transition from hyopsodontid to artiodactyl, the axis remained in about the same position. Further restriction of movement and greater joint stability was obtained in the latter through deepening of the tibial trochlea and further elaboration of the external and internal flanges on the distal end of the tibia. These flanges, the lateral one representing the last remnant of the well-developed hyop-

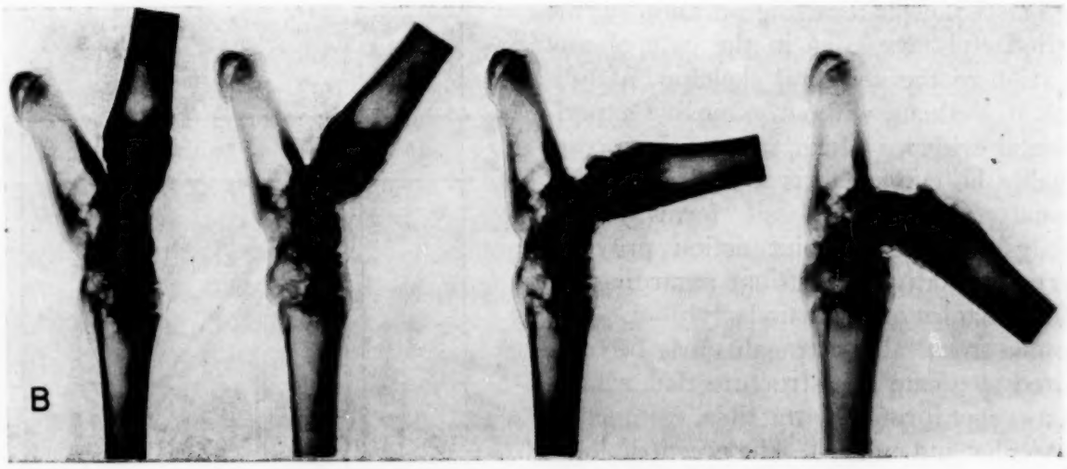

FIG. 4. Roentgenogram of the tarsal area of a living goat showing the rotation of the astragalus.

sodontid fibula, articulate with the tibia in a sort of tongue-and-groove relationship.

In contrast to the upper ankle joint, the lower ankle joint was subjected to a very radical change in orientation and function during the hyopsodontid-artiodactyl transition. In the generalized mammalian foot, including the hyopsodontid, the axis of rotation of the lower ankle joint has a very characteristic oblique orientation running in general from the dorsal surface of the neck of the astragalus to the lateral side of the heel process of the calcaneum. Movement is largely restricted to an inversion-eversion rotation of that portion of the foot below the astragalus, with the latter functionally united with the tibia by the presence of the tibial flanges and associated ligaments. In the artiodactyls, on the other hand, the change in the form of the astragalus and calcaneum previously discussed caused a shift in the orientation of the axis of the lower ankle joint to a position essentially parallel in all aspects to that of the upper ankle joint. There was during the hyopsodontid-artiodactyl transition, a change in joint motion from inversion-eversion of the foot to one involving only fore and aft rotation of the astragalus. This rotation occurs only during extension and flexion of the foot and cannot occur independently of movement at the transverse tarsal joint.

Motion at the transverse tarsal joint in the hyopsodontids involves two differently formed and rather complex articular surfaces. For the purposes of this discussion, however, the movement may be considered as essentially flexion and extension. The axis of this joint is almost parallel to that of the upper ankle joint. During the transition phase there was a simplification and structural convergence of the two articular surfaces (astragalus articulating with both the cuboid and navicular) with movement at the artiodactyl stage increased but practically limited to flexion and extension (fig. 4). The position of the axis suffered some reorientation which is of no particular significance in this discussion.

It is thus evident that the structural modifications in the tarsus during the transition period finally resulted in a unique arthrodial condition in which the axes of the three main tarsal joints have an essentially parallel orientation. This situation permitted, by the Lower Eocene, a freedom of movement on the part of the astragalus not present in any other order of mammals. A tendency in this direction did develop in some of the rodents, in the lagomorphs, and in certain of the extinct, neotropical, cursorial types such as the litopterns; the tarsus of these forms suggests resemblance to an intermediate stage in the hyopsodontid-artiodactyl transition.

The biomechanical significance of the artiodactyl tarsus, as in the case of any portion of the vertebral skeleton, is difficult to evaluate without extensive experimental evidence which, in turn, may reasonably be employed as a basis for functional studies on fossil forms. The analysis of tarsal joint action provides certain tentative conclusions regarding the biomechanics of the artiodactyl foot. The double-trochleated astragalus may be compared to a cam-like structure that rotates in a socket formed by the tibia, calcaneum, navicular and cuboid. The eccentric location of the cam axis, here the axis of the transverse tarsal joint, permits a greater degree of rotation at its proximal than at its distal end and has suggested to Kripp (1935) that the artiodactyl astragalus is, in effect, a velocity mechanism which increased the speed of rotation of the foot during flexion and extension. This is an adaptation of some significance in the cursorial artiodactyls as it must accelerate locomotion and, as part of this same effect, amplify the momentum imparted to the hind feet during the characteristic leaping stride.

The typical mammalian foot, including the hyopsodontid, when in contact with the ground, may be considered as a lever of the first class (Gregory, 1912), with the fulcrum located at the upper ankle joint, the power applied by the crural flexor muscles at the heel process and the resistance provided by the foot pressing against the ground. The leverage of the artiodactyl foot is complicated by the nature of the astragalus (fig. 5), which might be considered as an additional movable segment in the hind limb. With antero-posterior motion of the foot occurring at both the upper ankle joint and the transverse tarsal joints, it is possible to postulate the presence of two interrelated lever systems with separate fulcra, one at each of these joints.

In this compound lever system the force and resistance are still applied at the heel process and foot respectively. When the foot first touches the ground at the beginning of the propulsive phase, there is still some movement possible at the transverse tarsal joint although most of the extensor motion at this joint occurs prior to the contact. Observable motion at the upper ankle joint is initiated at this time. A lever analysis of this situation (fig. 6) indicates that at the onset of propulsion when maximum power is required the power arm (a′b′) of the more distal lever is longer than that (ab) of the proximal lever and the resistance arm of the former (b′c′) shorter than that of the latter (bc). There is thus a very slight but real mechanical advantage over the typical mammalian condition. Manter (1938), investigating locomotion in the cat, found that at the beginning of the propulsive phase of the hind limb a horizontal, longitudinal force produced by the resistance between the foot and the ground caused an actual retarding effect which was quickly overcome. That such an initial retarding effect is common to all tetrapods appears evident (Barclay, 1946) when the position of the entire hind limb in relation to the acetabulum is considered. The rapid and efficient overcoming of this negative action must be of prime importance in a

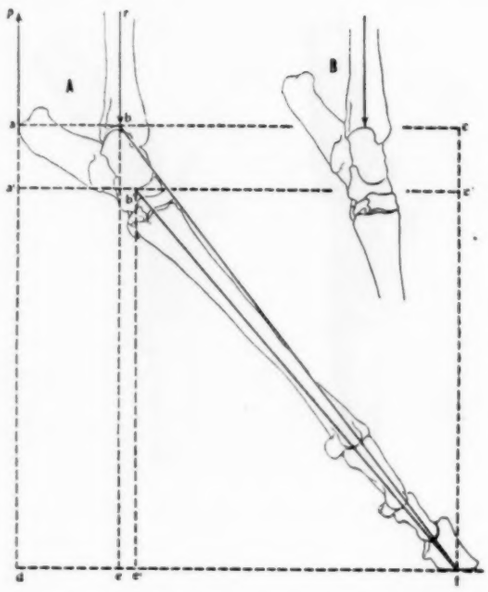

FIG. 5. A. Composition of forces in the artiodactyl hind foot oriented in the position assumed at the beginning of the propulsive stride. B. Position at the end of the stride.

cursorial mammal and the double lever effect in the artiodactyls may serve an important function in this regard.

The functional significance of any cursorial specialization is directly related to the ability of the animal to move at an initial and sustained speed great enough to permit escape from an enemy. In this connection it is, interesting to note that the limb ratios (for example, length of third metatarsal to length of femur) of most of the more generalized artiodactyls of the Tertiary and Recent fall within the range of the larger predatory carnivores. This overlap is ratios would place a high premium on the functional efficiency of the early artiodactyl tarsus, and its specialization prior to any marked increase in limb ratio clearly suggests its importance in this connection.

Evolutionary Implications

As pointed out earlier, ungulates, that may be identified as artiodactyls, apparently reached an ordinal status by the beginning of the Eocene. The primitive hyopsodontid condylarths, from which the even-toed ungulates were derived are first known from Lower Paleocene deposits. The transitional stage between hyopsodontid and artiodactyl, therefore, probably had a maximum duration of not over 15 million years according to the most recent opinions on the length of the Paleocene.

The time interval available for this transformation in tarsal design is brief according to paleontological standards and the rate of evolutionary change may be regarded as relatively rapid. The failure to discover any of the intermediate forms between the initiation and completion of the transition represents a situation that is common to the origin of nearly all the orders of mammals. Invariably the earliest representatives of a given order appear abruptly with one or more ordinal characters fully differentiated and there is good evidence for the belief that the preceding transitional period was tachytelic (Simpson, 1944).

Intensive collecting in deposits where transitional forms should occur but are actually absent suggests, although it does not necessarily prove, that these forms had a restricted geographical distribution throughout most of the transitional period. The taxonomic group involved in the transition was also undoubtedly limited, possibly to the specific level. There is slight reason for believing that intermediate forms may exist unrecognized in collections as all the known Paleocene faunas have been thoroughly studied and evaluated.

In order to explain this anomalous situation Simpson (1944), in a further extension and application of Wright's theories, has suggested as a hypothesis that mega-evolution usually occurs in small (in the Wrightian sense) populations subject to genetic drift. According to his concept, quantum evolution may account for the relatively rapid origin of higher categories such as families and orders. The non-adaptive change resulting from genetic drift that is characteritic of small isolated populations and usually brings about their extinction may, in very rare instances, actually be preadaptive for a different adaptive zone. The presence of preadaptation, which is a primary requirement, may thus permit the survival of the population and initiate its subsequent expansion at a new adaptive level. Quantum evolution is, as Simpson states, an all-or-none reaction; if the isolated population is unable to attain a new adaptive zone it will suffer extinction.

This concept of mega-evolution provides a possible explanation for two established facts in paleontology, the rapid and often radical transformation involved in the origin of many higher categories and the usual absence of specimens representing any level of the transitional stage. If the trend occurred in a small isolated, or probably even a small semi-isolated population, the chances of obtaining a sample by any available collecting technique are very remote (assuming that

some individuals in the poulation were preserved).

Simpson also points out that mega-evolution may occur in a less radical manner and actually intergrade with other modes of evolution, particularly phyletic. An evolutionary pattern possibly of significance in connection with the origin of the artiodactyls involves the appearance of preadaptation in a transitional population without the possible deleterious effect of genetic drift. Radical change in either member of the organism-environment equilibrium may ultimately produce a situation bringing about the extinction of the population or, in very rare instances, result in the quantum evolution effect. If the equilibrium changes without being lost, however, it indicates that the population has responded adaptively to environmental change. Thus a modification in the nature of the selection pressure can, under these circumstance, favor a new evolutionary trend with the critical transitional period between two adaptive zones being one of more or less continuous adaptation. Such a transition is more phyletic than quantum in its mode but may nevertheless approach the latter in rate and magnitude of change.

Certain features of the hyopsodontid-artiodactyl transition may reasonably be inferred on the basis of the known facts. In the early Paleocene a fairly large population of preartiodactyls, here considered to be primitive hyopsodontids, occupied a warm, moist, forested environment. The adaptive zone was relatively stable and the population was presumably subjected to only mild selection pressure. As must characterize all generalized ancestral stocks which give rise to higher categories, this one possessed a high degree of genetic plasticity with a potentiality for entering a variety of different adaptive zones. Sometime during the first half of the Paleocene some changing feature or features of the environment affected a particular segment of this hyopsodontid population. The nature of this change is unknown, but it is very reasonable to suppose that it was associated directly or indirectly with the evolution of the earliest carnivores, the creodonts. Although the Lower Paleocene creodonts and condylarths share many features in common, by the Middle Paleocene the creodonts were more specialized in a typically carnivore direction and became more efficient predators. This increase in the efficiency of the carnivores was, of course, intimately associated with the development of ungulate specialization and possibly both were related to some modification in the physical environment such as a tendency toward a more open plains habitat (there is actually no direct evidence of such change in the Paleocene) or to an expansion of the ungulates and carnivores into such an already existing habitat.

These generalized herbivorous hyopsodontids reacted to the increased predator pressure in a manner common to most ungulate groups by evolving a mechanism for faster locomotion. Why the tarsus was affected in this connection prior to any significant change in limb ratios or to reduction in the number of digits is an intriguing but at present unanswerable problem. As pointed out in the functional analysis, the tarsal modification increased the propulsive force exerted by the foot as well as accelerated the protraction and retraction phases of hind limb. This obviously had some initial selective advantage over those cursorial adaptations that were emphasized later in the Tertiary.

The evolution of the tarsus during the hyopsodontid-artiodactyl transition must have been essentially rectilinear and continuously adaptive. It seems reasonable to suppose that the effect of selection pressure on the new trend almost from the time of its inception was great enough to channel variation. The complexity of the tarsal joints and their intimate functional relationship certainly would not permit more than slight deviation in any portion of the complex without loss of efficiency, not to mention actual malfunction.

The evolution of the artiodactyl tarsus did not involve, in a broad sense, a complete change of function but rather a trend toward specialization and restriction of function. While it is true that the reorientation of the axis of the lower ankle joint did produce a marked modification in the function of the astragalus, there was no radical, basic change in the action of the foot as a whole in relation to its role in locomotion. It is therefore difficult or impossible to determine at what point in the transition the tarsus was preadaptive for a specialized cursorial function and, in fact, such a point probably did not exist. Along with the continuous adaptation of the tarsal complex for the precursorial environment there was a progressive preadaptation for the artiodactyl or cursorial one.

As the artiodactyl tarsus almost reached its biomechanical limit of specialization by the beginning of the lower Eocene, there was relatively little postadaptive change. The significance of the biomechanical limit has recently been discussed by Huxley (1942, p. 494). It represents that stage in an adaptive trend at which the greatest possible degree of mechanical efficiency is attained and beyond which further change can only be essentially nonadaptive. (It is, of course, not possible to prove that an actual biomechanical limit has been reached in a particular case although the weight of evidence may make it extremely probable.) If the limit is reached at a generalized level, however, as in the case of the primitive reptiles with their horizontally oriented proximal limb segments, it is possible to approach another and different limit by entering a new adaptive zone. In advanced mammal-like reptiles the entire limb assumed an almost vertical position permitting motion in a parasagittal plane. The biomechanical potentialities of this limb reorientation were so great that a number of different limits were now possible and were finally attained only in the many different groups of mammals ultimately derived from the therapsids.

The artiodactyl tarsus illustrates, on the other hand, the effect of extreme specialization in hastening the attainment of an apparently absolute limit. During the Tertiary, this order underwent a broad adaptive radiation which produced not only relatively conservative types but also extreme cursorial and graviportal forms. In all cases the tarsus remains amazingly similar. By way of postadaptive change there has been a relatively minor increase or decrease in the size of certain articular facets and a tendency toward fusion of the cuboid and navicular bones, probably refinements for somewhat greater mechanical efficiency and greater stability.

The pattern of evolution involved in the hyopsodontid-artiodactyl trend is obviously complicated, with different character complexes evolving at different rates and in response to different factors of the environment. The evolutionary change which is directly related to the origin of the Order Artiodactyla, however, apparently involved originally only a single character complex, the tarsus. Even in this restricted sense the mode is more phyletic than quantum in nature although there are features that indicate some intergradation between the two.

The taxonomic category resulting from the trend is at the ordinal level, a high level being characteristic of quantum evolution. There is, however, no indication of abrupt transfer from one adaptive zone to another but rather of the change occurring in a single shifting adaptive zone as in phyletic evolution. Adaptation in the precursorial zone was essentially continuous and was intimately associated with preadaptation for the cursorial zone. Post-adaptation was restricted in the cursorial zone by an early approach to the biomechanical limit of specialization. Presumably there was no particular point in the trend that might be considered as a threshold in the sense employed by Simpson (1944, p. 209) since there was no one morphological or functional stage that the tarsus had to attain in order to

prevent the actual elimination of the trend.

With the diagnostic features of pure quantum evolution absent, it is reasonable to assume that the population segment involved in the transition was semi-isolated, with some migration and cross-breeding between it and adjacent populations. Wright (1941 and elsewhere) has pointed out that rapid evolution can occur under these circumstances even to the extent of evolving a new higher category. Following Simpson's interpretation, this mode is essentially phyletic and involves less radical change than pure quantum evolution. The magnitude of change resulting from any adaptive trend, however, must be evaluated on a relative basis. The tarsus of terrestrial mammals has been modified into a limited number of rather distinct types, with that occurring in the Artiodactyla probably representing the greatest departure from the arctocyonid level. In terms of tarsal evolution in terrestrial mammals it is, therefore, a radical change effecting the entire economy of the animal. In terms of tarsal evolution in the mammals as a whole (including extreme arboreal and aquatic forms) it is much less radical but still great enough to form the basis for a new order through the reaching of a new adaptive plateau.

It appears evident that the character complexes that define and delimit the higher categories of organisms have not evolved at the same rate or necessarily at the same time. They apparently reached their definitive form in a regular sequence which for some orders of mammals can be estimated with reasonable accuracy. In the case of the even-toed ungulates the tarsus was apparently the first complex to attain this goal. The change in the orientation of the longitudinal axis of the foot from a position essentially along the third toe to one between the third and fourth toes may have occurred coincidently with the modification in the tarsus. This shift represents the appearance of another ordinal character. Its functional significance was not fully realized, however, until digital reduction involving the loss of the first toe and relative decrease in the size of the second and fifth toes was initiated in the Eocene in the various artiodactyl groups. Changes occurring exclusively at subordinal and lower levels also were started during the Eocene with diversification of the dentition probably beginning before there was any great alteration in limb ratios.

Summary

The character complexes of the various mammalian orders usually appear suddenly with no record of transitional stages from the presumed ancestral stock. The earliest members of the Artiodactyla are recognized positively on the basis of a single complex which is the highly specialized form of the tarsus. Basic similarity in the dentition of the Lower Eocene artiodactyls and a family of primitive Paleocene condylarths indicates that the latter represents the ancestral stock of the even-toed ungulates.

The transitional period from the primitive condylarths to the first true artiodactyls had a duration of not more than 15 million years. During this time there was a radical change in the form of tarsal elements and in the orientation of the axes of the three main tarsal joints. The resulting mechanism increased the speed of locomotion and probably reduced the retarding effect at the beginning of the propulsive stride.

According to paleontological standards the transition was rapid. It was also essentially rectilinear and continuously adaptive. Selection pressure, probably mostly predator pressure, channeled variation sharply during the entire trend. Preadaptation for the artiodactyl environment was a continuous process, occurring along with adaptation for the preartiodactyl one. The biomechanical limit of specialization for the tarsus was almost reached by the Lower Eocene, greatly reducing the possibility of modification in this complex during the Tertiary. The evolutionary

mode involved in the transition was essentially phyletic with some features attributed to quantum evolution.

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NATURAL SELECTION IN LABORATORY POPULATIONS OF DROSOPHILA *

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Introduction

L'Heritier and Teissier (1933) described a technique for maintaining laboratory populations of Drosophila at a fairly constant number with between three and four thousand flies always present in the population cage. The cage was a large box into which a container of food was placed every day or at regular intervals, a container in which the food had been exhausted being withdrawn each time one with fresh food was introduced. In this way a fairly constant food supply and the maximum population of flies which it would support, were maintained.

L'Heritier and Teissier carried out interesting experiments on competition between different species of Drosophila and between different mutant types and their wild type alleles. They did not exhaust, by any means, the possibilities of the technique in elucidating features of natural selection which could be studied in the laboratory.

Dobzhansky (1947 a, b and c) utilized the technique with success in demonstrating the response of different gene arrangements (inversions) in *Drosophila pseudoobscura* to different temperatures. In nature each gene arrangement occurs in populations of a definite geographic area. However, two or more gene arrangements may occur together in many populations. A particular inversion, if present, will be found in both the homozygous and heterozygous condition. According to Dobzhansky (1947b), "The relative frequencies of various gene arrangements in some populations undergo seasonal cyclic changes. These changes are produced by natural selection, and represent adaptive reconstructions of the population genotype, thus facilitating survival in different seasonal environments. Some of the changes taking place in nature can be reproduced experimentally in population cages in the laboratory."

It was shown that if a gene arrangement (inversion) called Standard is allowed to compete with another inversion called Chiricahua, both inversions, from flies collected at Pinon Flats, in population cages maintained at 20–25° C., that an equilibrium is established with about 70% Standard chromosomes as against 30% Chiricahua. The fact that equilibria of the various gene arrangements result from natural selection both outdoors and in the population cages, instead of complete replacement of one gene arrangement by another, indicates that the individuals heterozygous for different gene arrangements (inversion heterozygotes) have the highest adaptive values while the homozygotes are inferior to them in survival and reproduction. This "balanced polymorphism," resulting from the superiority of the heterozygote, preserves a few of the homozygotes of all types and thus permits the species to react adaptively to changes in its environment. The species is "buffered" against environmental change, and no hereditary variability is lost.

The present experiment which employs laboratory strains of *Drosophila melanogaster* was designed to demonstrate the superiority of an inversion heterozygote

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under exacting conditions such that the homozygous inversion was of poor viability and in competition was sterile. Obviously the chromosome containing the inversion would have been eliminated very soon in competition with a more normal chromosome unless the heterozygote had a distinct advantage over the homozygote lacking the inversion. If the inversion chromosome is able to survive in population cages for any length of time it will be because of an equilibrium formed dependent upon the superiority of the heterozygote over the homozygote types. The experiment was independent in conception from those of Dobzhansky just cited and was designed more as a test of theoretical considerations and to demonstrate the effects of accidental variation of gene frequencies rather than as a solution of the practical problems which Dobzhansky has answered, at least in part, as to why such a large array of inversion types have survived in wild Drosophila populations through the ages.

Materials and Methods

One of the early objectives of this study was to devise a population cage possessing certain advantages not provided by the model of L'Heritier and Teissier. A much more compact and easily handled unit with a smaller population was wanted. A cage was desired which gave some simulation of a seasonal cycle in regard to the food supply. Several models were made and the final product as used in the experiments to be reported seems to be highly satisfactory. The unit has been called a "population bottle."

The unit consists merely of two half-pint milk bottles, the mouths of which are connected by a three inch long section of rubber automobile radiator tubing. Each milk bottle has a paper cap perforated with two or three quarter inch holes which allow passage of the flies but prevent food and debris from being pushed from one bottle to the other by the larvae. There is a gap between the two bottles, inside the rubber tube, of about an inch, forming a small vacant chamber. There is a one-half inch hole in the rubber tube stoppered with cotton through which ventilation of the chamber and unit occurs. We are indebted to Mr. Ludwin for the discovery of the usefulness of automobile radiator tubing for this purpose.

Simple boxes lacking one side were constructed to hold ten units each, as shown in figure 1. As may be seen in the figure, the closed half of the box is painted black. When a cover is laid on top of the box one end still is open and thus the light attracts the flies into the bottle in the open, unpainted half of the box. These boxes may be piled upon each other thus permitting the storage of a large number of units in the small space usually available in incubators or constant temperature rooms. Many replications may be run at the same time. Our units were kept in a constant temperature room at $20.0 \pm 0.5°$ C.

The food material was the ordinary cornmeal-molasses agar which while still hot is poured into the bottles which are then laid on their sides. The food solidifies in a "slant."

The experiment was started with five pairs of flies in each of twenty slants without perforated caps or rubber tubes. When the population has flourished and begun to decline after two months, a perforated cap is inserted in the slant, the rubber tube with cotton plug and a new slant are added and we have a complete unit or "population bottle." The surviving flies of the population move into the new slant very promptly. The old slant remains attached for two additional months in order that the flies in the old slant which were in the egg, larval or pupal conditions may move into the new slant as soon as they emerge.

At the end of this time the four months old slant is removed, a new slant put in its place and the unit rotated 180 degrees so that the new food is always in the light half of the box, attracting the flies into the fresh slant.

Two or three days after the population

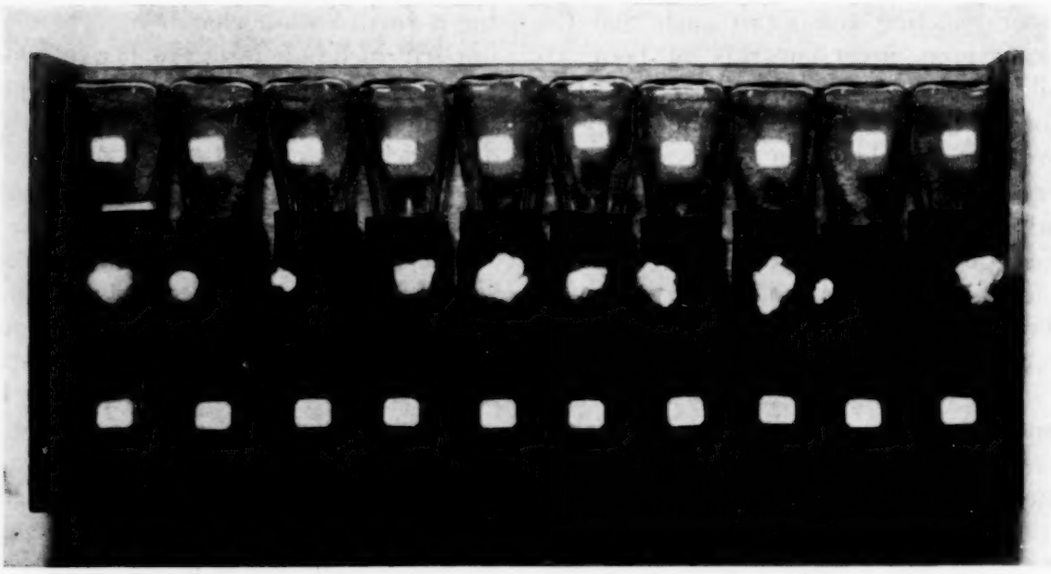

FIG. 1. Container holding ten population bottles. The cover for the box is not shown. Bottles in the dark half of the box are over two months old. The bottles in the left half have been attached for less than a week.

has moved into the new slant ether is dropped on the cotton "ventilator" and as soon as the flies in the new slant appear slightly "groggy" they are all removed, counted, and returned to the new slant, new cotton being placed in the ventilation hole. This means that the populations are always counted when at the lowest ebb. The breeding population is the smallest at the time of counting and consequently accidental variations in gene frequencies will be most important in these few flies which will be the parents of the first generation in the new slant.

At the time of counting, the population never numbered as many as 600 flies and as a result of more rapid deterioration of the food in some slants than in others an occasional population becomes extinct. One can afford to lose a population in this fashion every now and then in return for the assurance that all the surviving lines have passed through a period of adverse food conditions. More important, however, is the opportunity thus provided for random sampling to function. The population sizes in this experiment varied between one fly and 586, with an average of 161 flies per unit at the time of counting.

The two parental stocks which provided the competing chromosomes for this experiment were of the same species, *Drosophila melanogaster*. One strain is know as "Muller—5" or "M5". This strain has a long inversion in the X-chromosome which extends from the apricot locus to Bar. Both apricot and Bar are present and serve as "markers" or indicators of the presence of the inversion chromosome. For a more complete description of the M5 stock see Muller in D.I.S. 16. The chromosome in the particular strain used confers semi-sterility and poor viability upon the males which have it in the hemizygous condition and upon the females which are homozygous for it. M5 males are much less viable than males of the competing strain, white, miniature and forked. The combination of white eyes, miniature wings and forked bristles reduces vigor to a considerable extent but not nearly as much as genes present on the inversion chromosome. The presence of the inversion prevents crossing-over so that the two different chromosomes entering the competition should remain distinct indefinitely. However, crossovers do occur rarely and data from three of the

twenty-five population cages had to be discarded because of crossing-over.

The heterozygous female $\left(\frac{M5}{wmf}\right)$ has bean-shaped eyes of pale-apricot color and normal sized wings. The viability of these heterozygous females seems to be either as good or nearly as good as ordinary wild type females since 464 of the heterozygous and 485 of the wild type females were obtained in a test cross, with an expectation of equality.

Progress of the Competition

Twenty population bottles were started. In ten of them were placed heterozygous females $\left(\frac{M5}{wmf}\right)$ and large numbers of the semisterile males having the M5 inversion chromosome. Large numbers of the M5 males were needed in order to get crosses with the females heterozygous for the inversion. Presumably these vigorous females repulsed the advances of the weak M5 males. The other ten population bottles were made up with five of the inversion heterozygotes $\left(\frac{M5}{wmf}\right)$ and five white, miniature, forked (wmf) males. These five males were adequate to fertilize the heterozygous females. The immediate progeny from these crosses are expected to be of different types depending on whether M5 or wmf males were used. The following progeny of the ♀ ♀ $\frac{M5}{wmf}$ × ♂ ♂ M5 cross were obtained in the first generation:

Progeny:

♀ ♀ $\frac{M5}{wmf}$	♀ ♀ $\frac{M5}{M5}$	♂ ♂ M5	♂ ♂ wmf
64	34	33	63
33%	17.5%	17.5%	32%

Clearly the homozygous M5 ♀ has only about half the viability of the heterozygote.

In the other cross no homozygous M5 females are expected. The M5 males seem to be about one-third as viable as the wmf females which may be seen below.

Cross:

♀ ♀ $\frac{M5}{wmf}$ × ♂ ♂ wmf

Progeny:

♀ ♀ $\frac{wmf}{wmf}$	♂ ♂ wmf	♀ ♀ $\frac{M5}{wmf}$	♂ ♂ M5	Total
931	854	891	295	2971
31%	29%	30%	10%	100%

Each of the four classes in both crosses is expected to appear in a frequency of 25% but it is clear that homozygous M5 females and M5 males are significantly deficient in number.

In the first generation of the progeny from the crosses shown above all classes expected were represented, though not in full proportion because of poor viability of the M5 phenotypes. Natural selection began to function immediately, and at the end of two months the homozygous M5 females had disappeared completely from the population bottles. The M5 males had dropped in frequency to between 2 and 4% of the total population at the end of the two months. While a few M5 males appear in the population bottles at every count thereafter, they apparently fail to breed as not a single homozygous M5 female has been found among over 17,000 flies counted since the second month of the experiment. Such M5 females should have been produced if the M5 males succeeded in mating with the heterozygous females.

It is rather remakable that natural selection should have completed its main work by the end of the second month of competition in the population bottles. The high speed elimination of the homozygous M5 females leaves an equilibrium of three effective types of flies, the inversion heterozygotes, ♀ ♀ $\frac{M5}{wmf}$, the homozygous white, miniature, forked females and males. In addition about 2% of the ineffective M5 males are always to be found in the population bottles.

One might expect the inversion chromosome to be eliminated from the population bottles. However, the heterozygous $\frac{M5}{wmf}$ female is sufficiently more successful than the homozygous $\frac{wmf}{wmf}$ female so that the condition of heterozygosis is maintained.

The results of the counts from the two different crosses at intervals of about two months have been kept separate throughout the experiment. As the results from the two crosses were so nearly identical at the end of the second month it is not necessary to complicate the tables by showing the results of the two crosses separately; their combined totals will be given. The total number of flies drops with the passage of time due to the decrease in number of population bottles because of random extinction, breakage, mold infestations or other factors irrelevant to the experiment. The combined data are given in table 1.

Fluctuations of the Equilibrium

In other studies with these population bottles still in progress we started with a high precentage of white eyes versus red and got a rapid drop to low values of the white eye gene in the population. An advantage of the present cross is that an equilibrium is maintained with roughly equal percentages of each effective genotype present. Drastic changes in the conditions of the experiment would be necessary to cause radical fluctuations in the proportions of the different genotypes in the totals obtained from all the population bottles. Another advantage of this material is that every genotype may be rapidly and accurately determined by a glance at the phenotype. Classification was carried out with the aid of a dissecting microscope but it could have been done with the naked eye with only slight inconvenience.

The results of the competition between the two effective types of females, namely the homozygous $\frac{wmf}{wmf}$ and the heterozygous $\frac{M5}{wmf}$ are shown in table 1. As the 2% of M5 males offer no competition in mating there is only one kind of effective male, the wmf.

It seems clear that there has been an equilibrium of the three effective types of flies between the first count at the end of the first two months of competition and the last count at the end of fifteen months, perhaps shifted about by accidental variations in gene frequency and environmental fluctuations. The random deviations in gene frequency were beyond our control as were also the environmental fluctuations. Considering all the forces that could shift the equilibrium in one direction or another it is remarkable that the

Table 1. *The equilibrium established between the competing genotypes in the population bottles*

Date counted	♀♀ $\frac{wmf}{wmf}$	♂♂ wmf	♀♀ $\frac{M5}{wmf}$	♂♂ M5	♀♀ $\frac{M5}{M5}$	Total
7–15–46	822 (27%)	759 (25%)	1322 (44%)	118 (4%)	0	3021
9– 6–46	650 (31%)	630 (29%)	777 (37%)	50 (3%)	0	2107
11– 2–46	1047 (27%)	1009 (25%)	1840 (47%)	24 (0.6%)	0	3920
1–17–47	934 (28%)	1173 (35%)	1155 (35%)	57 (2%)	0	3319
2–25–47	438 (30%)	425 (30%)	549 (38%)	29 (2%)	0	1441
4–10–47	394 (29%)	462 (34%)	480 (36%)	12 (1%)	0	1348
6– 6–47	130 (22%)	129 (22%)	312 (53%)	19 (3%)	0	590
7–23–47	238 (22%)	193 (18%)	608 (56%)	45 (4%)	0	1084
8–27–47	132 (28%)	151 (31%)	191 (40%)	4 (1%)	0	478
Total	4785 (28%)	4931 (28%)	7234 (42%)	358 (2%)	0	17,308

maximum difference in the percentage of homozygous wmf females present at any two counts was no larger than 9%, the extremes having been 22% and 31%. With the heterozygous females somewhat larger fluctuations occurred, the lowest percentage having been 35% and the highest 56%.

Presumably this equilibrium could be maintained indefinitely. Not one population bottle of the twenty we started with has had to be discarded because of the loss of the M5 chromosome. If any flies survived at all, in exhausted bottles, at least one was heterozygous for the M5 chromosome.

Superiority of the Heterozygote

It will be recalled that in the first generation of the progeny from the cross of the heterozygous females $\left(\frac{\text{M5}}{\text{wmf}}\right)$ by white, miniature, forked males the proportions of the three effective types was about 30% of each. If there were no distinction between the homozygous wmf females and the heterozygous females in competition one might have expected random sampling of the M5 chromosome in subsequent generations with approximately three homozygous wmf females present in the population bottles for each heterozygous female.

Table 1 shows clearly that instead of a large excess of the wmf females there are always more of the heterozygous females, sometimes twice as many in the population bottles. The superior heterozygotes maintain themselves in excess as a result of the continuous action of natural selection within the population bottles.

The question comes up as to whether the heterozygous females could compete successfully with the homozygous females if greatly outnumbered by homozygotes. An experimental lot of ten population bottles was set up of which nine provided data. Heterozygous females were introduced in small numbers into populations of homozygous white, miniature, forked flies. At the first count, two months after the population bottles were set up, it was found that the heterozygous females had established themselves without difficulty as may be seen in table 2. At the end of the third count (six months) the heterozygous females accounted for 43% of the population which is in satisfactory agreement with the grand average of 42% for the experiment shown in table 1.

Table 2. *Introduction of a few heterozygous females* $\left(\frac{M5}{wmf}\right)$ *into larger populations of homozygous* $\left(\frac{wmf}{wmf}\right)$ *flies*

No. of population bottle.....	1	2	3	5	6	7	8	9	10
% ♀ ♀ $\frac{\text{M5}}{\text{wmf}}$ introduced	2	3	1	1	2	1	2	10	10
% ♀ ♀ $\frac{\text{M5}}{\text{wmf}}$ two months later	12	18	9	5	5	6	3	25	14

There can be no doubt that under the conditions in the population bottles, the possession of the M5 chromosome in the homozygous or hemizygous condition is equivalent to lethality whereas its presence in the heterozygous female is an advantage sufficient to prevent its extinction. If the populations were allowed to get so small that only one or two females survived, it is of course possible that they would be all wmf, and the M5 chromosome would be lost. Immigration would restore the favored type in a comparable situation in nature.

Accidental Variations

It has been pointed out in table 1 that the lowest average percentage of heterozygous females in all the population bottles at any one count was 35% while the highest count was 56%, a difference of 21%. As all the other differences are smaller, one might think that all the deviations from the grand average of 42% heterozygotes were purely random sampling fluctuations. However, when it is realized that each of these counts is for a large population of flies it should be clear

that the deviations are too large to be due entirely to chance fluctuations. This is demonstrated easily by finding χ^2 for the deviations of the number of heterozygous females observed from the number calculated on an expectation of 42% for the nine counts shown in table 1. Total χ^2 for the counts was 163.6 which is extremely large and gives an infinitely small probability that our counts are from a homogeneous population. Chi-square was also calculated for the 110 counts of individual population bottles using their deviations from the number expected for 42% heterozygous females. This value, using the $\sqrt{2\chi^2} - \sqrt{2n-1}$ arrangement, was 23.3 times its unit standard deviation and very highly significant. Most certainly the fluctuations are much greater than one would expect to result from random sampling of a homogeneous population. We must conclude that the population has changed its composition at times during the course of the experiment.

The most obvious place to look for radical fluctuations would be in the environmental conditions. Every reasonable precaution was taken to keep temperature and food conditions constant but the food conditions are quite beyond control because of the different sized populations which became established. There seems to be little doubt then that environmental fluctuations cause some of the variation in percentages of the three effective genotypes in individual population bottles.

Spencer (1947) gives evidence in *Drosophila immigrans* of genetic drift, presumably the result of near-extinction of small local populations during the winter with a great increase in frequency of some of the non-adaptive mutations during the following summer because they happened to have been present in the heterozygous condition in those few individuals which were the chance survivors of the winter season.

The conditions in our population bottles simulate the above situation to some extent in that often only a few individuals survive and pass into the new food bottles to become the parents of the next two or three generations, which are large because of the abundant food supply. There is a difference between our situation and that reported by Spencer. In our case genetic drift could barely get under way before selection would succeed in reversing the trend back toward the equilibrium.

There is no obvious way in which the shifts in frequencies of the two kinds of females can be evaluated as to that proportion of the shift which is due to environmental fluctuations and that due to accidents of sampling. There is at least one way, however, in which the presence of variability due to accidents of sampling can be demonstrated. This may be shown by the relationship between size of the population at the time it is counted and the change in gene frequencies at the next count. If variability due to sampling is important the greatest differences in frequencies should appear in populations which came from small numbers of parents. Consequently, the data to be presented show the change in percentage of heterozygous females $\left(\frac{M5}{wmf}\right)$ between any two counts in which there were at least an arbitrary total of forty flies in the later count. In other words, taking a single population bottle we find the difference in percentages of heterozygous females between the count at the end of the second month and the end of the fourth month and then plot this against the logarithm of the population size at two months. Next the difference in percentages of heterozygous females between the fourth count and the sixth count is then plotted against the logarithm of the population size at the end of the fourth month. This goes on until the span of time of the population bottle has been covered, then the data for the next population bottle are employed in the same way.

The resulting plot is shown in figure 2. It can be seen that with small numbers in

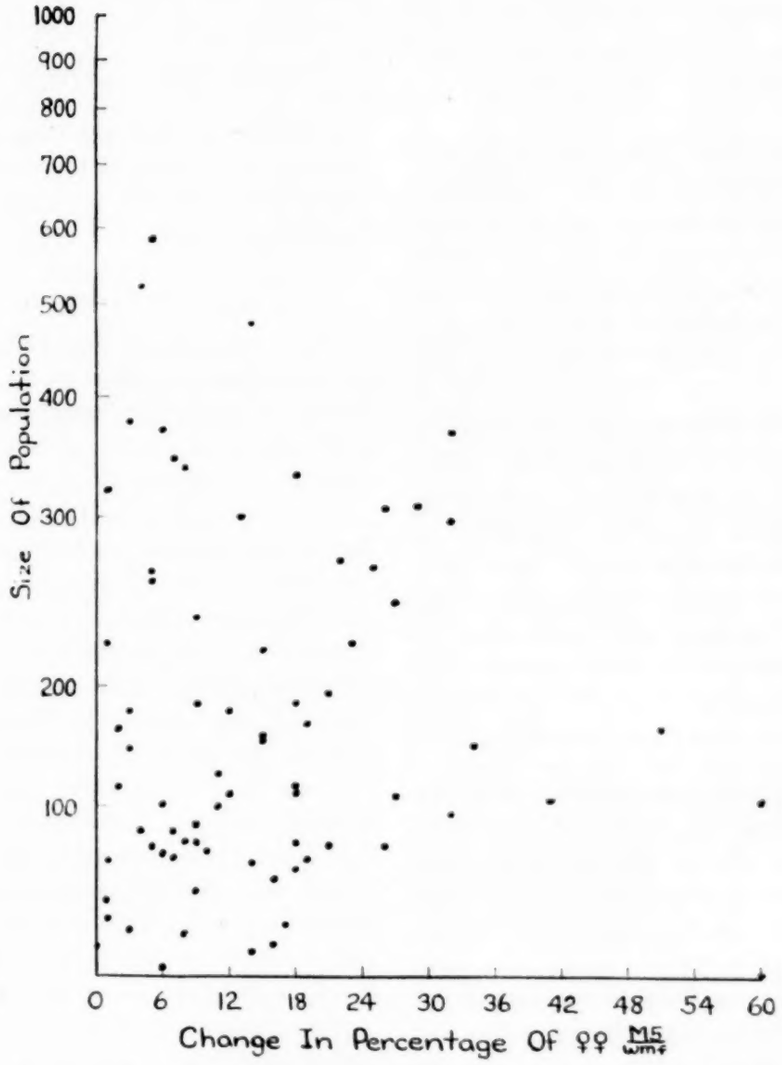

FIG. 2. A demonstration of accidental variation in gene frequencies. The larger the population the smaller the change in percentage of heterozygous females $\left(\frac{M5}{wmf}\right)$ during any one of the periods of two months.

the population which is ancestral to the flies counted two months later, a large fluctuation in the percentage of heterozygous females can occur in the individual population bottles. Five of the population bottles with less than 200 flies as a starting population showed between 34 and 61% change within the two months (this would mean from two to three generations of flies), but none of the bottles with more than 200 flies showed changes greater than 32%. Ten of the population bottles having between 200 and 400 flies at the starting count showed changes between 15 and 32%. The three bottles with starting counts of more than 400 flies showed changes of only 4%, 5% and 14%. It is quite clear that the larger the population maintained the less change there will be in the proportions of the M5 and wmf chromosomes in the two months period between counts. The smaller the population at the starting count the greater the change may be at the next count. The fact that this relationship holds is a demonstration of sampling variability at the population minimum which would result in "genetic

drift" except that in our experiment natural selection is too strong to allow much cumulative effect of the sampling variability.

We have a clear indication then, that under the conditions of our experiment sampling variation would not be of large magnitude in populations of over 1000 but it is certainly a major factor in the fluctuations exhibited in the populations descended from groups of less than 500 flies.

Further experiments are in progress with populations of about 500 – 2000 flies in order to obtain data concerning the magnitude of sampling variability in populations of this size range. It is possible to do this by substituting quart bottles for the one-half pint units used in this experiment.

Effect of Natural Selection

This experiment was designed with the expectation that the heterozygous female might have a strong selective advantage over the homozygous white, miniature, forked female. It has been pointed out already that this was decidedly the case.

Professor Sewall Wright has been most kind in calculating the selective value for the data and his estimate is that for the two month interval at which counts were made the selection values (W) were 0.286 for $\frac{\text{wmf}}{\text{wmf}}$ females as compared with 1 for $\frac{\text{wmf}}{\text{M5}}$ females. As there was more than one generation per 2 months interval the selection per generation is less than that just shown. If the average length of a generation were one month the values of W would be the square root of the figures above. Thus for $\frac{\text{wmf}}{\text{wmf}}$ females the value would be 0.535 to 1 for $\frac{\text{wmf}}{\text{M5}}$ females. If there are three generations during the interval between counts the values of W are the cube roots of the values for the entire 2 month period. In this case the value for $\frac{\text{wmf}}{\text{wmf}}$ females would be 0.659 and 1 for the heterozygotes. Considering either two or three generations Professor Wright's results show that the selection per generation is enormous.

Discussion

This laboratory experiment provides an analogous situation to a case observed widely in nature as "sex-ratio." In some wild strains of *D. pseudoobscura, D. persimilis, D. affinis, D. athabasca,* and *D. azteca,* Sturtevant and Dobzhansky (1936) found that certain males gave almost exclusively female offspring. Males carrying the "sex-ratio" X chromosome produced few sons, regardless of the female to which they were mated. Females, either heterozygous or homozygous for this X, produced a normal complement of sons and daughters when mated to normal males. Dobzhansky discovered that in *D. pseudoobscura* the "sex-ratio" factor was always associated with three inversions in the right limb of the X. The factor attains a frequency in the neighborhood of 20% in some populations.

An explanation of how this "sex-ratio" factor might be maintained in nature is apparent from our experiment. Presumably, the females heterozygous for "sex-ratio" and the three inversions have greater adaptive value than either homozygous type. This spreads the X with the "sex-ratio" factor on it through the population even though the "sex-ratio" factor would have negative adaptive value if it approached fixation, or perhaps considerably before then. The normal type male might have positive adaptive value in dispersal and in expanding populations where a higher proportion of males would be essential.

We assume that the gene arrangement has been preserved due to the existence of the inversions coinciding in position with the "sex-ratio" factor on the X chromosome.

Recently Novitski (1947) has proposed an interesting alternative explanation of the way in which the "sex-ratio" gene is maintained in the population.

We are most grateful to Professor Wright for having read the manuscript and for his contributions to it. We are likewise indebted to Professor Dobzhansky and to Dr. Novitski for having read the manuscript and for helpful suggestions.

Summary

A description is given of a new type of population cage, known as a population bottle, which has several advantages for a study of natural selection in laboratory populations of Drosophila. The population bottle is a small enough unit so that a number of replications of the experiment may be run simultaneously. The populations may be counted with ease, particularly as the counting is done when the population is at the ebb of its cycle. The populations expand greatly when a new food supply is made available at the end of each period of two months duration and become smaller as the amount and quality of the food decreases during the period of two months.

A competition was set up between an inversion X chromosome (M5, carrying markers apricot and Bar) and a "normal" X chromosome with the markers white eye, miniature wings and forked bristles. The inversion chromosome was of low viability and semi-sterile when in competition and for practical purposes could be considered to be a lethal, as homozygous M5 females were never found after the competition had been going on for as long as two months. There were always about 2% of the hemizygous M5 males present but apparently they never succeeded in mating and were ineffective. The effective males were white, miniature, forked. The females heterozygous for the inversion and the white, miniature, forked chromosome $\left(\frac{\text{M5}}{\text{wmf}}\right)$, and the females homozygous for white, miniature, forked were in competition.

One might expect the "lethal" inversion chromosome to be eliminated from the population bottles, but instead it flourishes in the heterozygous condition. The heterozygous female $\left(\frac{\text{M5}}{\text{wmf}}\right)$ is enough more successful than the homozygous female $\left(\frac{\text{wmf}}{\text{wmf}}\right)$ so that the condition of heterozygosis is maintained. An equilibrium was established with great rapidity and the composition of the population averaged 28% homozygous $\left(\frac{\text{wmf}}{\text{wmf}}\right)$ females, 28% hemizygous wmf males, 42% heterozygous $\left(\frac{\text{M5}}{\text{wmf}}\right)$ females and 2% hemizygous M5 males. These values fluctuated severely at times but without a trend.

It was shown that one of the primary causes for the fluctuations in the percentages of the various genotypes was the effect of accidental variations in the frequencies of the M5 and wmf chromosomes. In these population bottles where the population size was usually much less than 500, at counting, it is not surprising that random sampling was so important. The relationship found between population size at its minimum and the amount of accidental variation indicated that with populations in the neighborhood of 1000 or over, the effects of accidental variation would be small, at least during short periods of time.

The experiment was designed with the expectation that the heterozygous female might have a strong selective advantage over the homozygous female. This was found to be the case and Professor Sewall Wright has calculated the selective values which appear to be somewhere between 0.5 and 0.7 for the homozygous females compared with 1.0 for the heterozygous females each generation.

Three important sources of variability seem to exist in the populations of this

experiment. These three are environmental changes, accidental variations due to random sampling and strong selection pressure at each generation.

The analogy between this laboratory experiment and the "sex-ratio" condition found frequently in natural populations was pointed out.

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EXPERIMENTS ON SEXUAL ISOLATION IN DROSOPHILA. IX. BEHAVIOR OF MALES WITH ETHERIZED FEMALES

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Sexual isolation is very widespread between species of the genus Drosophila. When males and females of two or more species occur together the matings are predominantly or exclusively between representatives of the same species. Most experiments previously carried out to elucidate this phenomenon used the so-called multiple choice technique. Virgin females of two species are confined with males of one of them, and after a certain period of time all females are dissected and their tubular receptacles and spermathecae examined under the microscope for the presence of sperm. Such experiments establish the fact that sexual isolation is present, but give no information about the factors which make heterospecific inseminations rare or absent. In this respect, visual observations as made by Mayr (1946), Wallace and Dobzhansky (1946), and Spieth (1947), throw more light on the problem. A desired mixture of females and males of one or more species is placed together in a small, flat, glass cell, and their behavior is observed under a dissecting microscope. The various stages of courtship and copulation may be observed and recorded quantitatively. A similar technique has been used in the experiments reported in the present article. Dr. Irwin Herskowitz, of Columbia University, has found (unpublished) that males of *Drosophila melanogaster* may copulate with etherized females of their own species, and that such copulations result in apparently normal delivery of sperm. It has, therefore, been decided to test the behavior of males of some species of Drosophila when confronted with a choice of etherized females of their own and of alien species.

For this purpose, strains of *Drosophila pseudoobscura* and *D. persimilis,* collected at Lost Claim, California, and the Swedish-B wild-type strain of *D. melanogaster* have been used. Groups of about fifty males and females were aged separately for 7 days in vials with food in the case of *D. pseudoobscura* and *D. persimilis,* and for 3 days in the case of *D. melanogaster.* The males were then transferred in lots of three or four to fresh food vials. A day later one conspecific and one alien female were etherized and then introduced into the vial with the males. Females were etherized for as long as possible without killing them and remained unconscious for about twenty minutes. The ovipositors of the females were squeezed with a pair of fine forceps so that the two halves were not tightly closed during the course of the experiment. The results are summarized in table 1. The controls, also included in table 1, were set up in the same way substituting non-etherized females for the etherized ones. The difference in results, especially in the case of *D. melanogaster* males, is very striking. No choice is discernible when etherized females are used whereas only conspecific copulations occur with non-etherized females. Successful copulations were relatively easily obtained with *D. melanogaster* males but were much rarer with *D. pseudoobscura* males. The latter courted each other very actively but only rarely paid attention to the motionless females. The *D. pseudoobscura* males that were observed mounted the females in a normal position,

TABLE 1. *Number (n) of males which have copulated with etherized females, and per cent of females inseminated (%)*

n	males	females		% homospecific	% heterospecific
31	pseudoobscura	etherized pseudoobscura	etherized persimilis	55	45
30	pseudoobscura	pseudoobscura	persimilis	90	10
44	melanogaster	etherized melanogaster	etherized persimilis	45	55
40	melanogaster	melanogaster	persimilis	100	0

between the wings. *D. melanogaster* males mounted in all conceivable positions, belly to belly, or sideways. Separation was sometimes difficult and lasted several minutes. Upon dissection live sperm was found in the tubular receptacles of all etherized females that had been observed to copulate.

Copulation is the result of a chain of interdependent stimuli and reactions between the male and the female. A break in this chain might prevent the successful termination of copulation. In the light of our present knowledge such a break may occur in several ways:

1. The alien male does not give the necessary specific stimulus (smell, etc.), and there is no reaction on the part of the female such as the opening of the ovipositor. There may even be an antagonistic reaction such as kicking the male off.

2. The female gives a specific stimulus, sometime after the initiation of the copulation (secretion in the vagina, behavior, etc.), which differs from that of females conspecific with the male, and the male dismounts.

The situation may vary from species to species, or even in various populations of the same species; generalizations cannot be made from a few experiments.

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